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# Functional Anatomy of the Integument and Subcutaneous Structures of the Head, Neck and Thorax of the Domestic Turkey, Meleagris Gallopavo.

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# FUNCTIONAL ANATOMY OF THE INTEGUMENT AND SUBCUTANEOUS STRUCTURES OF THE HEAD, NECK AND THORAX OF THE DOMESTIC TURKEY, MELEAGRIS GALLOPAVO

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## ABSTRACT

The microdissection of the integument and subcutaneous structures of the head, neck, and thorax of the Domestic Turkey, Meleagris gallopavo, revealed a complex system with several distinct layers of connective tissue, smooth and striated musculature, and fat bodies (corpora adiposa). These layers show structural variations across the body surface, and the patterns of variation of the different layers correlate with one another. The smooth apterial muscles and the striated subcutaneous muscles complement each other in moving certain feather tracts. Fat tissue is deposited in the dermis as dermal fat, in the Fascia superficialis, and in distinct fat bodies associated with the F. superficialis and the constrictor layer. This fat tissue does not function only as an energy storage place but also as structural fat with crucial biomechanical roles. This study provides a first step towards taking a holistic approach to the study of the integument and subcutaneous structures and their biomechanical, physiological and structural properties.

# CHAPTER 1: INTRODUCTION

The integument and subcutaneous structures of vertebrates constitutes a complex organ system, which plays an integral role in osmoregulation, respiration, fat storage, and protection from mechanical trauma. In birds and mammals, the integument performs additional biological roles in thermoregulation and communication. In birds, especially, the integument has assumed a major role in locomotion through the large flight feathers, the remiges and retrices of the arm and tail. Though the literature on the vertebrate integument is extensive, a comprehensive understanding of the integument and the subcutaneous structures has not been achieved to the same extent as has been the case for other vertebrate organ systems (Moss 1972).

The integument of mammals, among all vertebrates, has been studied most extensively and intensively, mainly through histological methods (Maximow and Bloom 1953; Sajonski and Smollich 1972; Bloom and Fawcett 1975; Bargmann 1977; Hammersen 1980; Stenn 1983; Bacha and Wood 1990; Junqueira et al. 1992; Monteiro-Riviere et al. 1993; Walker and Homberger 1992, 1993; Walker and Liem 1994). In birds, however, the study of the integument has produced a less unified picture that is replete with contradictions and gaps in knowledge. This is because the skin of birds varies in its structure and function depending on the particular region of the body, the accessory integumentary structures it bears, and the particular underlying structures and organs. For example, the integument over the beak is hard and keratinized with a highly vascularized dermis with numerous touch receptors, the integument of the legs and feet forms keratinized scales, and the rest of the body's integument consists of soft epidermis that varies greatly in terms of the associated accessory and subcutaneous structures. The study of the avian integument and subcutaneous structures, therefore, has split into several specialized research programs with relatively little cross-fertilization. The only comprehensive treatise on the avian integument is the definitive handbook by Lucas and Stettenheim (1972), in which the entire literature dealing with the avian integument was reviewed, clarified, systematized, and augmented by new research.

Some of the various areas of specialization within the broad topic of the avian integument and subcutaneous structures comprise the histology of the cutis, i.e., the epidermis and dermis (e.g., Moser 1906; Greschik 1915; Belsky 1923; Clara 1923; Freund 1925, 1926a, b; Koutnik 1927; Lange 1927, 1928, 1929, 1931; Wodzicki 1927; Hassko 1929; Petry 1951; Bailey 1952; Ostmann et al. 1963; Jones 1971; Lucas and Stettenheim 1972; Stettenheim 1972; Hodges 1974; Sawyer et al. 1986), the surface anatomy of the skin (e.g., Lucas and Stettenheim 1965, 1972; McLelland 1991), the smooth feather muscles and their innervation as they pertain to the movement of feathers (e.g., Seuffert 1862; Jegorow 1887, 1890; Langley 1902a, b, c, 1904; Moser 1906; Morris 1956; Ostmann et al. 1963; Tetzlaff et al. 1965; Peterson and Ringer 1968; Lucas and Stettenheim 1965, 1972), the striated dermal musculature (e.g., Barkow 1829, Helm 1886, Fürbringer 1888, Shufeldt 1890, Kaupp 1918, George and Berger 1966, Vanden Berge 1975, Homberger and Meyers 1989), the development of the skin and feathers (e.g., Dantschakoff 1909;

Wassermann 1926; Clara 1929; Liebelt and Eastlick 1952, 1954; Rawles 1960; Ziswiler 1962; Golliez 1967; Sawyer and Craig 1977; Sawyer 1979a, b; Sawyer et al. 1984, 1986), the structure of feathers (e.g., de Meijere 1895; Sick 1938; Lucas and Stettenheim 1965, 1972; Spearman and Hardy 1985), the pigmentation of feathers (e.g., Völker 1936, 1937, 1942; Auber 1957a, b; Dyck 1966, 1971a, b, 1977, 1979, 1987, 1992; Brush and Power 1976), the pterylography (e.g., Beddard 1898; Clark 1898; Holmes 1935; Lucas and Stettenheim 1965, 1972; Clench 1970, 1985), the moulting patterns (e.g., Stresemann and Stresemann 1966, Palmer 1972, Payne 1972, Spearman and Hardy 1985, Brom and Dekker 1990), and finally the biochemistry of the epidermis and feathers (e.g., Brush 1976, 1980a, b; Brush and Wyld 1980, 1982; Homberger and Brush 1986).

All these studies have yet to be synthesized and integrated in such a manner as to provide a comprehensive picture of the avian integument, one that would explain the particularities of the avian integument as compared to that of other vertebrates. As Lucas and Stettenheim (1972) stated: "No adequate description of the chicken's skin is yet available in the literature."

The present study on the domestic turkey (Meleagris gallopavo) is aimed at starting on the path towards achieving this. At this point in time, it is possible to look at the integument and subcutaneous structures as a complex microanatomical organ in a holistic approach, while relying on well established histological data. The method of choice for such an undertaking is microdissection which allows a three dimensional visualization of complex structures over large surfaces. The study will concentrate on the integument of the head, neck, and thorax, excluding the rhamphotheca of the beak. Once the overall structural patterns are understood, specific sites of interest could be sampled for further studies using histological techniques.

The domestic turkey was chosen as the object of study for several reasons. Specimens of this species are readily available, and their large size facilitates the dissection of microscopic structures. The domestic turkey, being a member of the large family Galliformes, will also be able to serve as a base study for future comparative studies. Furthermore, except for some studies on the topography, pterylography, and feather muscle arrangement in comparison to those of the domestic chicken (Lucas and Stettenheim 1972, McLelland 1991), the integumental and subcutaneous structures of the domestic turkey have not been studied yet. The anatomical atlas on the domestic turkey by Harvey et al. (1968) does not address the integument.

This study will also revive and reinforce the notion that fat is not only an energy-storage tissue, but that it serves, perhaps equally importantly, as a filling and cushioning material with hydraulic properties and low metabolic demands for maintenance. Furthermore, this study is also a contribution towards understanding the relationship between smooth and striated subcutaneous muscles, and between feather and apterial muscles. The new information gathered in this study for the turkey will set the stage for acquiring a fresh understanding of the still poorly understood mechanism of feather movement.

## CHAPTER 2: MATERIALS AND METHODS

A total of three specimens of the domestic turkey, Meleagris gallopavo (Beltsville Broad-breasted White breed) were used in this study. Specimen DGH1 (female) was dissected in detail, and DGH2 (male) and DGH3 (male) were used to check for individual variations. The specimens were anesthetized by subcutaneous injection of Sodium phenobarbital (5-15 cc). After the specimens had lost consciousness, they were embalmed by perfusing 4% formaldehyde through the popliteal artery for 1-2 hours. The abdomen was separated from the thorax at the level of the caudal ends of the notarium and sternum, and the wings were clipped near the distal end of the humerus. In addition, the large contour feathers were clipped near their base to facilitate the dissection of the skin. The specimens were then submerged in 4% formaldehyde for 2-3 days before they were soaked in running tap water for about an hour to remove excess formaldehyde. The specimens were then transferred to a 2% phenoxyethanol solution for storage.

The dissections were done under Wild stereomicroscopes of the types M3Z, M8 and M3 with magnification ranges between 6x-50x, and fitted with a tube for dual observations, a fiber-optics ring light, and a polarizing light filter. A Volpi Intralux 6000 provided the light source. Dissection instruments consisted of stainless steel Dumoxel non-magnetic fine forceps (#4 and #5) and a pair of student vannas (i.e., spring microscissors).

The dissections were completed layer by layer, starting from the most superficial one to the deepest. Any incision was carefully planned and made so as not to damage any underlying structure or destroy some crucial anatomical evidence. An iodine solution (Bock and Shear 1972) was used to enhance the contrast between muscle and connective tissue. Because this solution does not differentiate between smooth and striated muscles, it was necessary to define structural aspects by which they could be distinguished. The smooth feather and apterial musculature is separated from the underlying striated subcutaneous musculature by the Fascia superficialis. The smooth musculature in the walls of blood vessels can be distinguished by its tubular arrangement and the tortuous path through the dermal and subcutaneous layers.

The interconnection between different layers was defined as fusion if the layers could not be separated without tearing holes in at least one of them. It was defined as a tight connection if layers could be separated, albeit with some difficulty. And it was defined as a loose attachment if the layers could be separated easily.

To study the relationship between the size of the feathers and the nature of the skin (see 3.3), the feather shafts of the ventral cervical and pectoral feather tracts were marked individually by creating a grid with black and white threads along the rows of feathers. In this way, each feather was identified by the crossing of two coordinates indicative of its position in the grid. The exact position of each feather was then mapped in a diagram. The relative size of individual feathers was established by measuring the long and short diameters of the cross-sections of the feather shafts near their base with the help of a graticle that was calibrated and inserted into one of the oculars of the stereomicroscope.

The anatomical nomenclature used here follows Lucas and Stettenheim (1972) and Baumel et al. (1993) whenever possible. Both Latin and Anglicized names were assigned to structures that were described for the first time, as well as to structures that previously had been given inappropriate names based on insufficient anatomical information.

The topography of the turkey was illustrated first as a basis for the rest of the anatomical descriptions. The figure was created by first making an outline of the turkey (specimen DGH1♀) with the help of an AM 200 Lucigraph optical enlarger/reducer. The structural details and corrections were added by hand to the outline by comparing it with the original specimen. The final rendering of the figure on topography (Figure 1) was made by an illustrator, and the black and white pencil drawing was then photographed and printed from a 4x5 negative. Each dissection stage was documented by mapping the individual layers on tracings of this initial figure. The mapping included the indication of the exact location of each structure and its variations. The structural relationships among the individual layers were analyzed by superimposing the diagrams of each individual layer. These structural correlations were then used as a basis for inferring hypotheses that would explain the regional differences of the individual layers. The final inked versions of the diagrams were made by an illustrator.

Photomicrographs were taken through the M8 Wild stereomicroscope by using a photoautomat and a MPS shutterpiece, as well as with a Volpi Intralux 6000 light source either with a fiber optics ring light and a light-polarizing filter, or with a pair of flexible goose-neck fiber optic light guides. The photoautomat coordinates several variables, such as light intensity, exposure time, and aperture of the shutterpiece. Since the anatomical object had a strong relief, as great a depth of field as possible had to be achieved by minimizing the aperture of the shutterpiece. However, a small aperture limits the amount of light reaching the object and requires longer exposure times, sometimes of several minutes. With longer exposure times, the normal vibrations that occur in a modern building would result in blurred photomicrographs. In order to avoid that, the photomicrographic equipment needed to be mounted on a TMC Micro-g vibration isolation table with an air pressure on the isolation legs of about 20-30 psi.

Whether the objects were illuminated with the ring light and polarizing filter or with the pair of goose-neck fiber optics light guides depended on the nature of the surface of the structures to be photographed. The ring light was better suited for a planar surface, whereas the goose-neck fiber optics light guides were better suited for an uneven surface with bulges and depressions. Due to its polarizing filter, the ring light contributes very little glare, but the photomicrographs lack a three dimensional aspect due to the uniform lighting and a lack of shadows. The goose-neck light guides provide the impression of three dimensionality due to the shadows they create but produce more glare. However, because the background vibrations were nullified by the vibration isolation table, the glare spots appeared small and sharply defined with no fussy boundaries that would obscure the structural details of the photomicrograph.

Before taking the photographs, the shutterpiece, the microscope, and the vibration isolation table were checked with a level for horizontality, and adjustments were made accordingly. To minimize the loss of depth of field, the specimen was set up in such a manner that the area that needed to be photographed lay parallel to the objective lens.

The composite photomicrograph was made by combining several photomicrographs, each of which depicts only a part of the entire area of interest. This method allows a larger area to be shown with more structural details than would be possible with a single photomicrograph. The main structural feature that needed to be photographed was put in focus and placed in the middle of a rectangular grid of a graticle that was inserted in one of the oculars of the stereomicroscope. The area that needed to be included in the composite was marked with pins and threads and moved along lines that paralleled the four sides of the rectangle. The photomicrographs were taken of the marked area in a systematic way so that any two consecutive photomicrographs could be overlapped in the final composite. Although overlapping is imperative to avoid gaps, it must not be excessive as it would result in too many lines indicative of the borders of the individual photomicrographs, which would interfere with the structural details of the composite. The photomicrographs were taken consecutively, and the same developmental procedures were used to ensure uniformity of intensity. For all the photomicrographs, T-max 100 Kodak film was used and push-processed to an exposure index of 200 to maximize the contrast.

The final composite was made by carefully overlapping the component photomicrographs. This was done by first sorting and arranging them in order to obtain an approximate construction of the final outcome. Then the photographs from the middle were chosen, joined, and fixed, two at a time, by using insect pins (size 00) passing through identical structures on each of the photomicrographs. In the case of photomicrographs taken with the goose-neck light guides, these structures were always well defined small glare spots. Once the overlapping points were identified and held together with pins, the photomicrographs were fixed with drafting tape on the underside of the photomicrographs. Once this was done, the pins were removed. The above procedure was repeated until the entire composite was constructed. The composite was then re-photographed to obtain the final print for publication.

# CHAPTER 3: ANATOMICAL DESCRIPTIONS

## 3.1. Topographic anatomy

Topographic anatomy is the description of surface structures and palpable structures underlying the skin, such as bones, the esophagus, the trachea, and the skeletomuscular vertebral column (see Figure 1). Many of these structures serve as landmarks in defining boundaries between regions of the body and as a framework for the description of the structural and functional relationships between the integument and the underlying subcutaneous structures.

### 3.1.1. Head

The head comprises the region from the tip of the beak to the caudal end of the underlying skull, which is at the level slightly caudal to the external ear opening (Apertura auris externa, Clark 1993a). The level of the boundary towards the neck is marked by the palpable occipital bones of the skull in the occipital region (Regio occipitalis, Clark 1993a) and the hyoid horn (Cornu branchiale, Baumel and Witmer 1993). The hyoid horn is part of the lingual apparatus and consists of the Os ceratobranchiale and the Os epibranchiale (Homberger and Meyers 1989). The beak is covered by the maxillary and mandibular rhamphothecae (Rhamphothecae maxillaris et mandibularis, Clark 1993b). The texture of the keratin of the rhamphotheca is not uniform; it is harder at the tip of the beak and becomes softer towards the root of the rhamphotheca (Radix rhamphothecae). The rictus (Clark 1993a) is the soft tissue joining the maxillary and mandibular rhamphothecae at the corner of the mouth. The keratinized, teardrop-shaped nasal operculum (Operculum nasale, King 1993) surrounds the external nasal opening and lies adjacent to the dorsal, caudally pointing wedge formed by the root of the maxillary rhamphotheca. The external ear opening lies caudodorsal to the caudal end of the palpable jugal bar (Arcus jugalis, Baumel and Witmer 1993). The jugal arch in both the wild and domesticated forms of the genus Meleagris, unlike that of other genera of Galliformes, bows outward and projects from the lateral side of the face (Shufeldt 1887, 1914). The ventral rim of the external ear opening is slightly raised above the surface of the lateral side of the head. The eye (Oculus, Clark 1993a) lies between the nasal operculum and the external ear opening, and its rostral border is at the level of the rictus.

The unpaired frontal process, or snood (Processus frontalis, Lucas and Stettenheim 1972), protrudes from the head middorsally and caudal to the nasal opercula. It is a cylindrical, fleshy process with a slightly flared base. The frontal process is short and unimposing in females (e.g., specimen DGH1♀; see also Timmer, no date), but is long (8-10 cm), prominent, and inflatable in mature males (e.g., specimens DGH2♂, DGH3♂; see also Lucas and Stettenheim 1972).

The dewlap (Palear, Habel et al. 1983) is a midventral fold of skin which extends from the level of the rictus down to the cervical caruncles (see below). It attains its maximum height caudal to the transition between the head and neck. In males, the dewlap is much more prominent than in females (see also Timmer, no date).

## 3.1.2. Neck

The neck is supported by the skeletomuscular vertebral column and is roughly sigmoid with dorsally convex curvatures near the head and near the thorax, and a ventrally convex curvature in the middle. The level of the caudal border of the neck is marked by the palpable shoulder joint, which is formed by the humerus, coracoid, scapula, and clavicle, and by the clavicle, which is palpable along its entire length.

The cervical caruncles (Carunculae cervicales) and the peduncle of the beard (Pedunculus barbae) are modifications of the skin. The cervical caruncles are large globular skin swellings on the lateroventral side of the neck. They extend from the cranial one quarter of the neck to the midlength of the neck and form a cluster of caruncles that are distinctly larger and more round than the more elongated caruncles of the adjacent caruncular skin (see 3.2.1.). The unpaired peduncle of the beard bears stiff, black keratinized filaments (see 3.2.2.1.) and is located on the ventral side of the neck just cranial to the region supported by the crop (Regio ingluvialis, Clark 1993a).

The neck shows a left-right asymmetry with respect to the positions of the esophagus and trachea. The esophagus is the continuation of the pharynx. It begins as a wide tube and gradually narrows starting at a level of two thirds of the distance between the hyoid horn and the cervical caruncles before it acquires a uniform diameter at the level of the cervical caruncles. The cranial one fifth of the esophagus lies on the midventral surface of the skeletomuscular vertebral column.

At a level slightly craniad to the cervical caruncles and where the vertebral column starts to curve ventrally, it turns to the right side of the neck and continues in this position down to the level of the shoulder joint where it expands into the palpable heart-shaped crop (Ingluvies, McLelland 1993), in which the apex points caudally and the base points cranially. The crop is positioned between the two clavicles and rests on an interlarded fascial sheet that bridges the clavicles. The trachea continues caudad from the larynx in the floor of the pharynx as a tube with a uniform diameter. The cranial one fifth of the trachea lies midventrally on the ventral surface of the esophagus then turns to the right side of the neck, where it follows the ventral side of the esophagus. The trachea remains close to the esophagus down to a level slightly craniad to the peduncle of the beard, where it begins to diverge from the esophagus and turn towards the left side of the neck. At a level slightly caudal to the peduncle of the beard, it begins to curve back again towards the midventral line. In doing so, the trachea follows the left cranial border of the heart-shaped crop before it enters the thoracic cavity. The trachea is palpable to the level of the peduncle of the beard before it begins to diverge from the esophagus. The esophagus is not easily palpable, but the crop is.

The neck begins to expand gradually at the level of the cervical caruncles. It attains a maximum width where it borders the thorax at the level of the clavicles.

### 3.1.2. Thorax

The thorax starts cranially at the level of the shoulder joint and the clavicle and is supported by the underlying rib cage and its musculature. The caudal end of the notarium (Baumel and Witmer 1993), which consists of four thoracic vertebrae, and the caudal end of the sternum mark the boundary between the thorax and the abdomen. The palpable shoulder joint lies in the dorsal half of the lateral side of the thorax at the level of the clavicle. The region of the shoulder joint (Regio omalis, Clark 1993a) is surrounded by feather tracts (see. 3.3.1.) except on the caudal half of its dorsal side where it is bordered by a skin fold that is part of the larger prepatagium of the wing (sensu Lucas and Stettenheim 1972) and on the dorsal one third of the caudal side where it hugs the subhumeral apterium (sensu Lucas and Stettenheim 1972) of the base of the wing.

The base of the wing (Basis alaris) is located caudal to the Regio omalis. The dorsal side of the base of the wing is covered by the scapular region (Regio scapularis). The scapular region is underlaid by the scapular bone which lies across the rib cage. The middorsal thoracic region is raised and underlaid by the spinous processes of the notarium and its musculature. The scapular region is separated from the middorsal region by a longitudinal depressed region that bears the scapular apterium (see 3.3.2.3.). On the ventral side, the base of the wing lies in a slight depression, the axillary depression, on the side of the thorax. The palpable pectoral musculature underlies most of the lateroventral aspect of the thorax. It covers a large area to include the arm pit region (Regio axillaris), which lies cranial and ventral to the base of the wing, the slightly depressed region caudal to the pectoral muscle (Regio retropectoralis), and the region underlaid by the palpable keel of the sternum (Carina sterni, Baumel and Witmer 1993) and its apex (Apex carinae, Baumel and Witmer 1993).

3.2. Integument

Only the macroscopic aspects of the epidermis are described here; the microanatomical aspects are described in section 3.4.

3.2.1. Surface texture of the integument

The skin occurs in three main types of surface textures: Smooth, wrinkled, and caruncŭlate. These skin types represent main stages along a gradual trend towards greater surface texturing.

Smooth skin is defined as skin without any protuberances. It covers most of the body, except the head, the cranial part of the neck, the beak, and the lower parts of the legs that are covered by scales.

Wrinkled skin is textured by small, elongated protuberances that are separated by fine grooves. It covers a large part of the head and the cranial part of the ventral side of the neck. The border between the wrinkled and caruncŭlate skin starts rostrally from the caudal end of one operculum and continues caudally dorsal to the eye and external ear opening. It then curves at some distance from, but around, the external ear opening and hyoid horn and extends along the neck down to the cervical caruncles to cover the ventral one sixth of the circumference of the neck, which covers the palpable trachea (see Figure 2). The area covered by the wrinkled skin actually corresponds to the combined area of the ophthalmic, gular and auricular feather tracts (see Figure 3; and 3.3.1.1.). The caruncŭlate skin is distinguished from the wrinkled skin only by degrees in that the protuberances are much more distinct and form elongated or globular caruncles. The cervical caruncles are the largest ones and measure about 20 mm x 12.5 mm. Rostrally, the carunc6ulate skin starts middorsally between the nasal opercula and continues as middorsal band along the dorsal border of the wrinkled skin to cover the occipital region and most of the cranial one third of the neck all the way to the caudal border of the cervical caruncles, except for the ventral band of wrinkled skin overlying the trachea, a middorsal wedge of smooth skin projecting rostrally up to the level of the cranial border of the cervical caruncles, and a wider midventral wedge of smooth skin projecting cranially between the cervical caruncles. The area covered by the carunculate skin corresponds to the area of the occipital feather tract (see Figure 3; and 3.3.1.1.).

3.2.2. Accessory integumentary structures

3.2.2.1. Beard filaments

The beard filaments are keratinous and arise from dermal papillae on the peduncle of the beard. They are stiff, black, and are not modified feathers (for details, see de Meijere 1895, Boas 1931, Schorger 1957, Lucas and Stettenheim 1972).

3.2.2.2. Feathers

The structure, size, and distribution patterns of the different types of feathers play a crucial role for this study as they correlate with many of the structural variations of the integument and underlying subcutaneous structures. Only a brief characterization of the various types of feathers is included here since they have already been described in detail by Lucas and Stettenheim (1972).

A feather has two major parts, namely the calamus, which is embedded in the skin within the feather follicle (see 3.4.3.), and the rachis, which projects above the surface of the skin. The latter is the shaft of the feather and bears primary and secondary branches (barbs and barbules, respectively) which form the vane of the feather. The barbules can either interlock and form the pennaceous part of the feather, or they can be free and form the plumulaceous part of the feather. In general, the plumulaceous part is located towards the base of the feather, and the pennaceous part is located towards the tip of the feather. The size and proportion of the two parts vary among different types of feathers. The feathers are categorized into six basic types based on characteristics of the rachis and vane, though they often intergrade from one feather type to the other. Feathers are, therefore, not always easily assigned to a particular type. In addition, there is considerable overlap in sizes among the different types of feathers as reflected by the length and diameters of the raches (see Table 1). The cross-sectional area of the rachis is not circular, but slightly compressed between the upper and under sides of the feather. The barbs attach to the lateral surfaces of the rachis and, thus, across its longer diameter. Because the feathers move in a generally longitudinal plane as they rotate cranially when raised and caudally when lowered, the short diameter of their rachis lies along a longitudinal axis of the body, and their long diameter along a transverse axis.

Contour feathers: A contour feather is a "typical" feather with a distinct rachis, and barbs that originate along the entire length of the rachis and decrease in length from the base to the tip of the rachis. The large flight feathers and tail feathers (remiges and rectrices, respectively) are entirely pennaceous and lack a plumulaceous part, but the rest of the contour feathers comprise both parts.

The contour feathers are classified for the specimen DGH1♀ used in this study as "small" if their rachis has a long diameter less than 1.00 mm near the base of the vane, and as "large" if it has a diameter equal to or greater than 1.00 mm. The critical size distinguishing "small" from "large" feathers, however, changes with the size of the specimen and the relative size of its feathers. Small contour feathers usually have not only a relatively narrow and short rachis but also a relatively large plumulaceous part. Conversely, large contour feathers usually have not only a relatively thick and long rachis but also a relatively large pennaceous part. It is the presence of even the smallest pennaceous portion in the vane that distinguishes a contour feather from a semiplume. In the turkey, contour feathers are found only in feather tracts. All feather tracts, except the gular and ophthalmic feather tracts, bear contour feathers.

Semiplumes: A semiplume differs from a contour feather by having an entirely plumulaceous vane. It resembles a contour feather in having the barbs originating from the entire length of the rachis. In the turkey, semiplumes are restricted to the apteria. They are lacking, however, from the sternal apterium, from a strip of the trunk apterium caudal to the axillary feather tract and dorsal to the caudal end of the pectoral feather tract, and from the caudal two-thirds of the scapular apterium.

Bristles: A bristle is a feather characterized by a relatively long rachis and a few short barbs that are confined to the base of the rachis. The number of barbs in a bristle may vary from one or two to as many as twenty or more. The barbs can be pennaceous, plumulaceous, or both. By definition, the longest barb is shorter than half the length of the rachis. A bristle, therefore, appears needle-like. In the turkey, bristles are found only in the gular feather tract (see 3.3.1.).

Semibristles: A semibristle is a feather that is intermediate between a bristle and a contour feather. It resembles a bristle in having its barbs originating only from the basal half of the rachis, but differs from a bristle in having the longest barb exceeding half the length of the rachis. The barbs can also be pennaceous or plumulaceous, although they are more commonly plumulaceous. A semibristle has a bushy appearance distinguishable from the more needle-like appearance of a bristle. In the turkey, semibristles are confined to the ophthalmic feather tract (see 3.3.1.).

Filoplumes: A filoplume consists of a very fine rachis and a tuft of short barbs at the tip of the rachis. Filoplumes are always associated with the much larger contour feathers and semibristles. They are not included in the later descriptions as they do not possess their own feather muscles and are very thin. Their follicles are surrounded by mechanoreceptors (Herbst corpuscles), and they are thought to measure the movements of other feathers (Golliez 1967, Lucas and Stettenheim 1972).

Down feathers: A down feather lacks a rachis or has only a very short rachis that is shorter than the longest barb. Its vane is entirely plumulaceous. In the turkey, only a few down feathers occur on the upper and lower eye lids and are interspersed among the semibristles of the ophthalmic feather tract.

### 3.3. Pterylography

Feathers are not evenly distributed on the skin, but concentrated in definite feather tracts (pterylae) which are separated from one another by areas that are bare or bear only semiplumes (Lucas and Stettenheim 1972). Feathers are inserted obliquely in the skin, generally with the feather follicle pointing cranially and the rachis and vane pointing caudally. These feathers can be raised, depressed, or rotated individually or in groups by smooth feather muscles. Entire feather tracts can be drawn closer to each other by smooth apterial muscles which attach to peripheral feather follicles along the borders of feather tracts and form a continuous layer with the smooth feather musculature (see 3.5.). In addition, feather tracts can be moved by striated dermal muscles which may attach to the skin or to individual feather follicles along the periphery of feather tracts (see 3.7.). Thus, subcutaneous structures co-vary with the pattern of feather distribution, which needs to be established in order to elucidate any functional significance of this co-variance.

The individual feather tracts vary in the type, size and density of the feathers they bear, and in the nature of the underlying subcutaneous structures. Of the six types of feathers discussed earlier (see 3.2.2.), only semiplumes do not occur on the feather tracts studied here.

The size of feathers within a feather tract can vary remarkably. For example, the difference in the long diameter of the rachis base between the smallest and largest feather is nearly fifteen fold (see Table 1), and the difference in length is more than a thousand fold (Lucas and Stettenheim 1972). In general, the size of feathers within a particular feather tract increases from cranial towards caudal and decreases from the center of the feather tract towards its periphery.

The nature of the skin and subcutaneous structures, varies with the size of the feathers they support. Large feathers are implanted in skin areas that are underlaid by clearly delimited and externally recognizable subepidermal pads of fat tissue ("subdermal fat bodies" of Lucas and Stettenheim 1972). As was established for the specimen DGH1♀ in this study, any feather with a long diameter of the rachis base equal or larger than 1.00 mm was implanted within a region underlaid by a subepidermal fat pad (see 3.3.1.2.). Feathers with a long diameter of the rachis base less than 1.00 mm were implanted outside or within the periphery of an area underlaid by a subepidermal fat pad. Thus, the value of 1.00 mm for the long diameter of the rachis base was taken as the critical value to separate "small" from "large" feathers in this specimen. This critical value, however, varies with the individual animal and its size.

The density of feathers can vary within and among feather tracts. According to Lucas and Stettenheim (1972), the three features of feather size, subepidermal fat pad, and feather density can be used to classify particular feather tracts as being either "strong" (i.e., large feathers, subepidermal fat pad present, and high feather density) or "weak" (i.e., small feathers, no subepidermal fat, and low feather density). For the domestic turkey, however, this classification cannot be applied as the three characters seem to vary rather independently from one another in the various feather tracts.

Feather follicles within a particular feather tract are arranged in rows, except in the gular feather tract, the caudoventral part of the occipital feather tract, and the central area of the ophthalmic feather tract. In the dorsal cervical, ventral cervical, interscapular, scapular, and pectoral feather tracts, the rows are diagonally arranged relative to the longitudinal and transverse axes of the body. These axes change their orientations in different parts of the body as they follow the bulges, depressions, and curvatures of the body surface. In this diagonal arrangement of feather follicles, the segments of the intersecting rows form parallelograms of which each corner is marked by a feather follicle. The diagonals crossing these parallelograms lie parallel to the longitudinal and transversal axes. In the auricular feather tracts, the feather follicles are arranged in concentric rows, whereas in the ophthalmic feather tract, only the peripheral feathers are arranged in rows that follow some borders. In the dorsal and sternal feather tracts, the arrangement of feather rows is more complex and could not be studied, as the abdominal portions of these feather tracts had been removed from the specimen.

The nomenclature of Clark (1993b) for the pterylae and apteria was adopted with some modifications. For example, each clearly definable region of feather tracts and bare regions was termed a feather tract (pteryla) or an apterium, respectively, even if they were part of a larger feather tract or apterium. The justification of this approach is that the pterylae and apteriae so defined frequently correlate with cutaneous and subcutaneous areas and structures. In the head region, the pterylae were defined according to the skin type and feather type they bear. This modification ensures that each feather tract of the head is characterized by a uniform population of feathers as are the feather tracts of the body, which bear mainly contour feathers besides filoplumes. Furthermore, the Pteryla scapulohumeralis was renamed "Pteryla scapularis" as it lies on the thoracic region of the body external to the scapula and is not part of the wing. The Apterium truncale laterale was subdivided into Apterium axillare cranial to the axillary feather tract and an Apterium truncale caudal to the axillary feather tract (see Figure 3).

As the size and density of feathers determine the nature of the underlying subcutaneous structures, the description of functional relationships among the various cutaneous and subcutaneous structures is facilitated by integrating the feathers as one of the factors in this study.

### 3.3.1. Feather tracts (Pterylae)

The pterylae are concentrations of feathers that are separated by apteria, except on the head and cranial part of the neck where the feather tracts lie adjacent to one another. These pterylae bear only small feathers and, therefore, do not need neighboring apteria. In defining the borders of the feather tracts, it is necessary to mention some of the apteria; these are, however, described in detail later (see 3.3.2.).

3.3.1.1. Capital feather tracts (Pterylae capitales)

The four capital feather tracts are defined by three feather types and two skin types (see Figures 2 and 3). Two of these feather tracts extend onto the cranial part of the neck.

Auricular feather tract (Pteryla auricularis): The circular auricular feather tract (Pt.aur) bears small contour feathers on wrinkled skin (see Table 4). It encircles the external ear opening and is completely surrounded by the gular feather tract (see later). The auricular feather tract is characterized by large feathers, a subepidermal fat pad, and a high feather density. The feathers are arranged in two concentric rows encircling the external ear opening.

Ophthalmic feather tract (Pteryla ophthalmica): The ophthalmic feather tract (Pt.oph) bears semibristles on wrinkled skin and is restricted to the rostrolateral region of the head (see Table 4, Figure 2). It embraces the caudal borders of the nasal operculum, follows the root of the maxillary rhamphotheca to the rictus, and continues towards the external auditory meatus by following the underlying, palpable jugal bar (see Figure 2). Before reaching the external auditory meatus, the ophthalmic feather tract turns rostrodorsally in a sharp angle towards the eye where it follows the dorsal side of the eye as a narrow band, and finally turns medially towards the middorsal line between the nasal opercula. The ophthalmic feather tract is surrounded by the gular feather tract, except rostrally where it is bordered by the nasal operculum and the maxillary rhamphotheca.

The ophthalmic feather tract is characterized by small feathers, no subepidermal fat pad, and a high density of feathers. Rostrally and dorsally, the peripheral semibristles are arranged in rows that follow the contours of the borders of the nasal operculum, maxillary rhamphotheca, and eye; towards the center and caudoventrally, the semibristles are arranged in no particular order.

Gular feather tract (Pteryla gularis): The gular feather tract (Pt.gul) bears bristles on wrinkled skin (see Table 4, Figure 2). It covers the ventral and part of the lateral sides of the head and extends along the ventral side of the neck down to the cervical caruncles. The gular feather tract encloses the ophthalmic feather tract and completely surrounds the auricular feather tract. The gular feather tract starts as a band from the ophthalmic feather tract at a level caudal to the frontal process. By following the dorsal border of the ophthalmic feather tract, it continues in a wide curve around the auricular feather tract, and covers the entire gular region ventral to the palpable jugal bar. The cervical extension of the gular feather tract down to the cervical caruncles covers only the ventral one sixth of the circumference of the neck, which is underlaid by the trachea. The gular feather tract is bordered by the occipital feather tract along its entire dorsal border, by the cervical caruncles on its caudal border, and by the mandibular rhamphotheca and the ophthalmic feather tract rostrally. The contralateral gular feather tracts meet along the midventral line.

The gular feather tract is characterized by small feathers, no subepidermal fat pad, and a high density of feathers. The bristles are arranged in no apparent order.

Occipital feather tract (Pteryla occipitalis): The occipital feather tract (Pt.occ) bears small contour feathers on carunculate skin and covers the dorsal sides of the head and cranial one third of the neck (see Table 4, Figure 2). Rostrally, the middorsal occipital feather tract is wedged between the nasal opercula, briefly skirts the ophthalmic feather tract and the base of the frontal process, and continues caudally by following the dorsal border of the gular feather tract all the way to the cervical caruncles. The contralateral occipital feather tracts meet along the middorsal line from the root of the maxillary rhamphotheca down to about the level of the cranialmost cervical caruncles, where they are separated by the cranially projecting wedge of the dorsal cervical feather tract. The divided contralateral occipital feather tracts then curve ventrally to cover the entire cluster of cervical caruncles, where they meet along the midventral line. Ventral to the caudalmost cervical caruncle, they are separated by the wider cranially projecting wedge of the ventral cervical feather tract (see later). Caudally, the occipital feather tract borders the lateral cervical apterium.

Rostrally and along the entire middorsal region, the occipital feather tract, quasi as a rostral extension of the dorsal cervical feather tract (see later), is characterized by having small feathers, no subepidermal fat pad, and a high density of feathers. Its feathers are arranged in rows that are oriented diagonally to the longitudinal axes which follow the contours of the head and cranial part of the neck. The lateral side of the cranial part of the neck caudal to the external ear opening, is characterized by having small feathers, no subepidermal fat pad, and a low density of feathers. Its feathers are not arranged in any particular order. They are present on the cervical caruncles and in the grooves between them with no more than two feathers per caruncle.

3.3.1.2. Cervical feather tracts (Pterylae cervicales)

Dorsal cervical feather tract (Pteryla cervicalis dorsalis): The dorsal cervical feather tract (Pt.ced) bears contour feathers on smooth skin (see Figures 2 and 3). It is the cervical part of the unpaired spinal feather tract (sensu Lucas and Stettenheim 1972) which runs along the middorsal line of the entire neck and thorax. It begins as a narrow wedge between the contralateral occipital feather tracts at a level slightly cranial to the cranial border of the cervical caruncles, but acquires a uniform width of about the dorsal one fourth of the circumference of the middle of the neck, which it maintains throughout its course along the neck. At the level of the palpable clavicle, it continues caudally as the interscapular feather tract (see later). Along its ventral border, the dorsal cervical feather tract is separated from the ventral cervical feather tract (see next) by the lateral cervical apterium, except at its very cranial end, where the two cervical feather tracts are separated by the caudal end of the occipital feather tract.

The cranially projecting wedge of the dorsal cervical feather tract is characterized by small feathers, no subepidermal fat pad, and a low feather density. However, at the level of the caudal border of the cranial one third of the neck above the midlength of the cervical caruncles, it is characterized by having large feathers, a subepidermal fat pad, and a high feather density. The rows of feather follicles are arranged diagonally relative to the longitudinal axes that follow the curvature of the dorsolateral side of the neck. The diagonal lines across the parallelograms lie parallel to the longitudinal and transversal axes of the feather tract. The rows of the contralateral dorsal cervical feather tracts form a chevron pattern in which the middorsal apices of the chevrons point cranially. The borderline between the weak and strong parts of the feather tract lies transversely across the chevrons.

Ventral cervical feather tract (Pteryla cervicalis ventralis): The ventral cervical feather tract (Pt.cev) bears contour feathers on smooth skin (see Table 4; Figures 2 and 3). It begins as a cranially projecting wedge between the cervical caruncles and runs along the ventral one third of the circumference of the neck. When it approaches the caudal one third of the distance between the cervical caruncles and the peduncle of the beard, it expands laterally and reaches its maximum width and caudal border at the level of the palpable clavicle (see Figure 3). At this point, the ventral cervical feather tract bifurcates dorsally into the narrower scapular feather tract and ventrally into the wider pectoral feather tract (see later). The contralateral ventral cervical feather tracts meet along the midventral line up to the caudal end of the peduncle of the beard. Farther caudally, they are separated by the Apterium cervicale ventrale, which covers the region underlaid by the crop.

The ventral cervical feather tract can be subdivided into two clearly delimited parts, namely into a strong and a weak feather tract part. The strong feather tract part is underlaid by a thick subepidermal fat pad and bears feathers with the long diameter of their rachis base measuring mostly 1.00 mm or more. Along its periphery towards the weak feather tract part, it comprises a few individual feathers with the long diameter of their rachis base measuring less than 1.00 mm (see Table 2). The strong feather tract part covers the entire wider caudal part of the ventral cervical feather tract with a small cranial projection into the narrower cranial part, but does not reach the midventral line cranially from the caudal end of the peduncle of the beard. The weak part of the ventral cervical feather tract has no subepidermal fat pad and bears only feathers with a long diameter of less than 1.00 mm (see Table 2). The weak part covers the narrower cranial part of the feather tract with a cranially projecting midventral wedge between the caudal half of the cervical caruncles; another midventral wedge extends caudally to the caudal end of the peduncle of the beard between the contralateral strong parts of the ventral cervical feather tract.

The measurements of the feathers in the ventral cervical feather tract clearly indicate that feathers with a long diameter of their rachis base of 1.00 mm or more, or with a short diameter of 0.85 mm or more, do not occur in areas that lack a subepidermal fat pad (see Tables 2 and 3). This suggests that there is a functional reason for the correlation between the occurrence of the large feathers and the presence of a subepidermal fat pad.

The rows of feather follicles are arranged diagonally to the longitudinal axes that follow the contours of the body (see Figure 4A). The rows of feather follicles in the unpaired cranial five eighths of the ventral cervical feather tract form a chevron pattern in which the apices of the chevrons point caudally.

3.3.1.3. Thoracic feather tracts (Pterylae thoracales)

Some of the thoracic feather tracts are extensions of the cervical feather tracts and some others are separated from them by apteria.

Interscapular feather tract (Pteryla interscapularis): The interscapular feather tract (Pt.isc) bears contour feathers in smooth skin (see Figures 2 and 3). It is the paired thoracic portion of the spinal feather tract (sensu Lucas & Stettenheim 1972) as well as the caudal extension of the unpaired dorsal cervical feather tract (see Figure 2). Cranially, the interscapular feather tract starts at the level of the shoulder joint and ends at the level of the caudal border of the base of the wing. The interscapular feather tract is bordered by the scapular apterium along its ventral and caudal borders. The contralateral feather tracts are separated from each other by the very narrow, middorsal, unpaired spinal apterium. Along the middorsal line, the caudal end of the interscapular feather tract connects with the cranially projecting middorsal extension of the dorsal feather tract (see next) via a single row of feathers (this connection is not visible in Figure 3).

The interscapular feather tract is characterized by large feathers, a subepidermal fat pad, and a high feather density. The arrangement of the feather follicles continues the pattern established by the dorsal cervical feather tract. The feather follicle rows are arranged diagonally relative to the longitudinal axes that follow the dorsal curvature of the thorax above the notarium of the vertebral column and the scapular bone. The diagonal lines crossing the parallelograms are parallel to the longitudinal and transverse axes of the body. As in the dorsal cervical feather tracts, the feather rows of the contralateral interscapular feather tracts form a chevron pattern, and the apices of the chevrons point towards cranial. The apices of the chevrons, however, are formed by the semiplumes of the spinal apterium (see later), which separates the contralateral scapular feather tracts.

Dorsal feather tract (Pteryla dorsalis): The dorsal feather tract (Pt.dor) consists of contour feathers in smooth skin (see Figures 2 and 3). It is unpaired and covers the dorsal part of the caudal region of the trunk and represents the cranial portion of the dorsopelvic feather tract (sensu Lucas and Stettenheim 1972). In this study, only its thoracic portion could be studied. Cranially, it is separated from the interscapular feather tract by the caudalmost transverse portion of the scapular apterium, except for a single row of feathers projecting cranially on the middorsal line and establishing a bridge with the interscapular feather tract and the spinal apterium (this connection is not visible in Figure 3). Its cranioventral corner touches the caudal border of the scapular feather tract. Along its cranioventral border, it is flanked by the trunk apterium. The contralateral dorsal feather tracts meet along the middorsal line.

The dorsal feather tract is characterized by large feathers, a subepidermal fat pad, and a high feather density. The feathers are arranged in a complex pattern of rows, which could not be analyzed because only the thoracic portion of the feather tract was available.

Scapular feather tract (Pteryla scapularis): The scapular feather tract (Pt.sca) bears contour feathers on smooth skin (see Figure 2). It is the narrower caudodorsal extension of the ventral cervical feather tract and covers the bulging shoulder region over the scapular bone (see Figure 3). The scapular feather tract parallels the interscapular feather tract; both feather tracts begin cranially at the level of the palpable clavicle and shoulder joint and end caudally at the level of the caudal end of the base of the wing (see Figure 3). The scapular feather tract is bordered medially by the scapular apterium and laterally by the humeral apterium of the wing (sensu Lucas and Stettenheim 1972). The caudal end of the scapular feather tract borders the dorsal feather tract and the trunk apterium.

The scapular feather tract is characterized by large feathers, a subepidermal fat pad, and a high feather density. The feather follicles are arranged in diagonal rows with respect to the longitudinal axes that follow the bulging shoulder region over the scapular bone. The diagonal lines crossing the parallelograms lie parallel to the longitudinal and transversal axes of the scapular feather tract.

Pectoral feather tract (Pteryla pectoralis): The pectoral feather tract (Pt.pec) bears contour feathers on smooth skin (see Figure 2). It is the wider caudoventral extension of the ventral cervical feather tract, starting cranially at the level of the clavicle and covering an area in the middle of the thorax between the base of the wing and the keel of the sternum (see Figure 3). It is bordered dorsally by the axillary apterium and the axillary feather tract; dorsocaudally by the trunk apterium, and ventrally by the pectoral apterium.

The pectoral feather tract is characterized by the large size of its feathers and the presence of a subepidermal fat pad. However, it varies in the density of feather follicles. In the cranial four fifths of the pectoral feather tract, the feathers are less densely arranged than in the caudal one fifth, where they are more densely arranged (see Figure 4A). The feather follicles are arranged in rows that are oriented diagonally relative to the longitudinal axes of the body. The longitudinal axes of the pectoral feather tract closely follow the contours of the bulge formed by the underlying pectoral musculature. Therefore, the longitudinal axes tend to curve dorsally towards the caudal end of the pectoral feather tract. The diagonal lines crossing the parallelograms formed by the crossing rows of feathers lie parallel to the longitudinal and transversal axes (see Figure 4A).

Axillary feather tract (Pteryla axillaris): The axillary feather tract (Pt.axi) consists of contour feathers on smooth skin (see Figure 2). It is located between the caudal half of the base of the wing and the pectoral feather tract. Cranially, it is bordered by the axillary apterium and caudally by the trunk apterium (see Figure 3).

The axillary feather tract is characterized by large feathers, but no subepidermal fat pad, and a low density of feathers. Its feathers are arranged in rows that are oriented diagonally relative to the longitudinal axes of the body.

Sternal feather tract (Pteryla sternalis): The sternal feather tract (Pt.ste) consists of contour feathers on smooth skin (see Figure 2). It is a separate feather tract on the ventral surface of the trunk lateral to the keel of the sternum. Cranially, it starts caudal to the apex of the sternal keel at twice the distance between the clavicle and the apex of the sternal keel (see Figure 2). It widens gradually as it extends caudally towards the abdomen. Craniodorsally and dorsally, it is bordered by the pectoral apterium and ventrally by the sternal apterium.

The sternal feather tract begins as a feather tract with large, but widely spaced feathers and without a subepidermal fat pad. Caudally, it gradually changes into a feather tract with more densely arranged feathers as it extends onto the abdomen. Only the weak thoracic portion could be included in this study. The feather follicles are arranged in rows that are oriented diagonally relative to the longitudinal axes of the body.

3.3.2. Areas with semiplumes or no feathers (Apteria)

3.3.2.1. Capital apteria (Apteria capitalia)

The head lacks any apteria and, therefore, the four feather tracts on the head are adjacent to one another.

3.3.2.2. Cervical apteria (Apteria cervicalia)

Lateral cervical apterium (Apterium cervicale laterale): The lateral cervical apterium (Apt.cel) bears semiplumes and runs between the dorsal and ventral cervical feather tracts on the lateral side of the neck (see Figure 2). Cranially, it borders the curved caudal end of the occipital feather tract. At the level of the palpable clavicle and shoulder joint, it continues caudally as the scapular apterium (see Figure 3).

Ventral cervical apterium (Apterium cervicale ventrale): The unpaired ventral cervical apterium (Apt.cev) beard semiplumes and begins cranially at the caudal border of the peduncle of the beard. It covers the region underlaid by the crop (see Figures 1 and 2). It is bordered dorsally by the ventral cervical feather tract and caudally by the cranial end of palpable clavicle which marks the border of the pectoral apterium. The contralateral apteria merge along the midventral line (see Figure 3).

3.3.2.3. Thoracic apteria (Apteria thoracalia)

Scapular apterium (Apterium scapulare): The scapular apterium (Apt.sca) bears semiplumes in its cranial one third, but is bare in its caudal two thirds (see Figure 2). The scapular apterium is the caudal extension of the lateral cervical apterium and starts at the level of the palpable clavicle and shoulder joint (see Figure 3). It separates the ventral border of the interscapular feather tract from the dorsal border of the scapular feather tract. At its caudal end, it curves medially and narrows to a point near the middorsal line (this is not visible in Figures 2 and 3). It separates the lateral three fourths of the caudal border of the interscapular feather tract from the cranioventral border of the dorsal feather tract, except for the middorsal bridge between these two feather tracts.

Spinal apterium (Apterium spinale): The spinal apterium (Apt.spn) is restricted to a narrow ribbon that bears a single row of semiplumes. It lies middorsally between the paired contralateral interscapular feather tracts. Cranially, it is bordered by the unpaired dorsal cervical feather tract. Caudally, the spinal apterium is connected to the cranially projecting middorsal extension of the dorsal feather tract (this is not visible in Figures 2 and 3).

Pectoral apterium (Apterium pectorale): The pectoral apterium (Apt.pec) bears semiplumes and borders the ventral edge of the pectoral feather tract (see Figure 2). Cranially, the palpable clavicle marks its border towards the ventral cervical apterium. Caudally, the ventral border of the pectoral apterium is flanked by the sternal feather tract (see Figure 3). Cranial to the sternal feather tract, the ventral border of the pectoral apterium is established by the cranial extension of the ventral border of the sternal feather tract towards the ventral edge of the palpable clavicle.

Sternal apterium (Apterium sternale): The sternal apterium (Apt.ste) is the unpaired bare region that covers the region covering the keel of the sternum (see Figures 2 and 3). It is framed by the pectoral apteria cranially and the sternal feather tracts caudally. Cranially, it is separated from the ventral cervical apterium by the palpable clavicle. The sternal apterium extends caudally and merges with the median abdominal apterium (sensu Lucas and Stettenheim 1972). Only the thoracic portion of the sternal apterium could be studied.

Axillary apterium (Apterium axillare): The axillary apterium (Apt.axi) bears semiplumes and is located in the axillary region. Cranially, it is bordered by the caudal border of the ventral cervical feather tract, ventrally by the dorsal border of the pectoral feather tract, caudally by the axillary feather tract, and caudodorsally by the base of the wing (see Figures 2 and 3).

Trunk apterium (Apterium truncale): The trunk apterium (Apt.tru) has two parts: A bare cranial strip adjacent to the caudal border of the axillary feather tract, and a caudal part that bears semiplumes. The trunk apterium covers the dorsal half of the retropectoral region of the thorax (see Figures 1, 2, and 3). Dorsally, it is bordered by the dorsal feather tract, cranially by the caudal end of the base of the wing (the caudal tip of the posthumeral tract sensu Lucas and Stettenheim 1972) and the axillary feather tract, and cranioventrally by the pectoral feather tract. Beyond the caudal end of the pectoral feather tract, the ventral border of the trunk apterium towards the pectoral apterium is established by the caudal extension of the ventral border of the pectoral feather tract (see Figures 2 and 3). The trunk apterium extends caudally as the lateral pelvic apterium (sensu Lucas and Stettenheim 1972) onto the abdomen, but only the thoracic portion of the trunk apterium was studied here.

3.4. The microanatomy of the skin (Cutis)

The microanatomy of the skin reveals regionalized features due to various modifications of the skin, such as caruncles, dewlap, and the frontal process (see 3.2.), and the regionalization of feather distribution in pterylae and apteria (see 3.3.). In addition to the regionalized features that correspond to these surface structures, the microanatomy of the skin correlates with subcutaneous structures, such as the superficial fascia (see 3.6.), the constrictor layer (see 3.7.), and some of the deeper structures and organs. Depending on the region of the body, the skin varies considerably in the thickness of the dermis, the amount of fat deposited in it, and the structure of the smooth musculature in it.

The skin consists of the outermost epidermis and the deeper dermis (Moser 1906; Greschik 1915; Clara 1923; Freund 1925, 1926a, b; Koutnik 1927; Lange 1927, 1929, 1931; Wodzicky 1927; Petry 1951; Bailey 1952; Ostmann et al. 1963; Jones 1971; Lucas and Stettenheim 1972; Stettenheim 1972; Hodges 1974). The feather follicles are part of the skin and are formed by both the epidermis and dermis; therefore, they will be described separately.

### 3.4.1. Epidermis

The epidermis is the thin outermost layer of the cutis. The finer subdivisions of the epidermis are not discernible at the magnification levels used in this study. The epidermis is tightly attached to the Stratum superficiale of the dermis (see next), as these two layers usually come off together during dissection, although it is possible to separate them mechanically under high magnification.

### 3.4.2. Dermis

At the levels of magnification used for this study, only a superficial and a deep layer of the dermis could be distinguished. The Stratum superficiale is tightly interwoven and, therefore, often called Stratum compactum. The Stratum profundum consists of a looser connective tissue and contains fat in varying amounts. It can be very easily separated from the overlying Stratum superficiale. However, there is no sharply defined borderline between the Stratum superficiale and the Stratum profundum (see Figure 6).

The pattern of dermal fat distribution in the Stratum profundum (Figure 5) is correlated with the pterylosis as well as with some subcutaneous structures. There are two obvious trends in the pattern of dermal fat distribution. First, there is more dermal fat in the thorax as compared to the head and neck. Second, without exception, the feather tracts and their parts that are characterized by large feathers, a subepidermal fat pad, and a high density of feathers also contain more dermal fat than other regions (see Figure 5). In fact, the dermal fat is part of the subepidermal fat pad. In addition, a large amount of dermal fat is also found in the axillary feather tract, along the ventral border of the base of the wing overlying the Corpus adiposum axillare of the constrictor layer, and in the trunk apterium, the caudal half of the thoracic part of the pectoral apterium, as well as in the scapular apterium craniad to the cranial border of the underlying M. latissimus dorsi cranialis (sensu Vanden Berge 1975), and within the peduncle of the beard.

There is only a minimal amount of dermal fat found in the feather tracts of the head and in the narrow midventral region overlying the keel of the sternum (see Figure 5). Little dermal fat is found in most of the lateral cervical apterium, in the ventral cervical apterium, in most of the part of the ventral cervical feather tract that is characterized by small feathers, no subepidermal fat pad, and a high density of feathers, in most of the sternal apterium except its midventral region, and in the dorsal half of the axillary apterium. An intermediate amount of dermal fat is found in many transitional areas between areas with large or small amounts of fat. It is characteristic for the cranial part of the dorsal cervical feather tract which is characterized by small feathers, no subepidermal fat pad, and a high density of feathers. It is also characteristic for the sternal feather tract, the cranial half of the pectoral apterium, and the caudal part of the scapular apterium caudad to the cranial border of the underlying M. latissimus dorsi cranialis (sensu Vanden Berge 1975).

3.4.3. Structure of the Feather Follicles (Folliculi pennae)

The wall of the feather follicle is formed by the epidermis and the Stratum superficiale of the dermis (see Lucas and Stettenheim 1972, Stettenheim 1972). The feather is held firmly within the feather follicle, as the epidermis forming the wall of the feather is continuous with the epidermis of the feather follicle (see Figure 6). The pulp cavity at the base of the feather follicle is filled with dermis which carries blood vessels and nerve endings (Boas 1931, Dreyfuss 1937, Hodges 1974). As a feather ages, the pulp cavity and the dermis within regresses towards the base. The Stratum profundum of the dermis is a thick layer where it surrounds the feather follicle but is thin near the base of the feather follicle where the blood vessels and nerves enter the pulp cavity.

The smooth feather and apterial muscles (Stratum musculare viscerale; see 3.5.) form a layer between the Stratum profundum of the dermis and the underlying F. superficialis. They are enveloped by a distinct epimysium-like elastic lamina, which is especially thick on its side towards the F. superficialis. The feather muscles are oriented obliquely relative to the apterial muscles (see 3.5) and the pars pennarum of the striated subcutaneous muscles (see 3.7.). For clarity, only two types of feather muscles, the M. erector and M. depressor, are shown in Figure 6, although there may be additional muscles present depending on the feather tract. The tendons of the feather muscles attach to the wall of the feather follicle, by fusing to the Stratum profundum as does the epimysial Lamina elastica (Lucas and Stettenheim 1972).

3.5. Smooth dermal muscle layer (Stratum musculare viscerale)

The smooth musculature of the skin comprises the feather muscles as well as the apterial muscles. Earlier studies and textbooks (Seuffert 1862; Jegorow 1887, 1890; Langley 1902a, b, c, 1904; Moser 1906; Boas 1931; Morris 1956; Ostmann et al. 1963; Tetzlaff et al. 1965; Peterson and Ringer 1968; Lucas and Stettenheim

1965, 1972) describe the two types of muscles as structurally quite distinct, but related histologically, functionally, and positionally. The feather muscles form muscle bundles that interconnect and move feather follicles within pterylae and are embedded within the dermis. The apterial muscles, in contrast, form muscle sheets that underlie apteria and attach to feather follicles along the periphery of feather tracts.

This study shows, however, that the fiber bundles of the feather and apterial muscles are part of the same muscular layer and that they are surrounded and interconnected by a very delicate, though strong sheet of elastic connective tissue lying between the Stratum profundum of the dermis and the Fascia superficialis. This sheet of connective tissue was described, though not understood in its structural significance, by Lange (1931) as well as by Lucas and Stettenheim (1972) and named "elastic membrane".

The anatomy of the feather muscles in relation to the feather follicles has already been studied extensively (Lucas and Stettenheim 1972, and references therein) and, therefore, needs only to be briefly redescribed within the new frame of reference described in this study. In contrast, the apterial muscles have received little attention by avian anatomists other than a brief mention when they are especially thick and dense (see Osborne 1968, Lucas and Stettenheim 1972). This study is the first one to examine all apterial muscles in the neck and thorax of the domestic turkey.

3.5.1. Feather muscles (Mm. pennarum)

The fiber bundle-like feather muscles attach to feather follicles by means of tendons that appear white and transparent (see also 3.4.). The tendons at each end of a single feather muscle attach to two adjacent feather follicles (see Figure 6). Each feather follicle is usually connected to four neighboring feather follicles by feather muscles in such a manner that the feather muscles form parallelograms of which each angle is marked by one feather follicle. Feather muscles are usually obliquely oriented relative to the longitudinal and transversal axes of the body, which results in the typical bias pattern of feather follicle arrangement within feather tracts (see Figure 4; see also Lucas and Stettenheim 1972).

The particular site of attachment on the feather follicle depends on the function of the muscle. According to Lucas and Stettenheim (1972), three types of feather muscles are recognized on the basis of their function: Depressor muscles (Mm. depressores), erector muscles (Mm. erectores), and retractor muscles (Mm. retractores). Erector muscles run from the neck of one feather follicle to the base of one of the feather follicles craniolaterally to it, and depressor muscles pass from the neck of one feather follicle to the base of one of the feather follicles caudolaterally to it (see Figure 6). Retractor muscles pass from the neck of one feather follicle to the neck of an adjacent one. Thus, a bunch of muscle fiber bundles connecting two adjacent feather follicles usually comprises all three types of feather muscles as they attach to a particular feather follicle. A fourth type of feather muscle, i.e., diagonal muscles, is occasionally present. It runs diagonally across the center of individual parallelograms formed by the other feather muscles. If diagonal muscles are present, such as in the ventral cervical feather tract, they are oriented along the longitudinal axes of the body. Also, a single feather follicle is then connected to six other feather follicles.

The feather muscles appear to be embedded within the Stratum profundum of the dermis. However, each bunch of muscle fiber bundles connecting two adjacent feather follicles is enveloped by a thin sheet of elastic connective tissue (see Greschik 1915, Lucas and Stettenheim 1972). This connective tissue represents quasi the epimysium and perimysium of the feather muscles. It also extends as a membrane (or fascia) across the center of the parallelograms circumscribed by the feather muscles and is anchored to each enveloped bunch of feather muscle fiber bundles, as it continues at their "epimysium". In other words, the feather muscles are built into a continuous connective tissue sheet which lies between the Stratum profundum of the dermis and the Fascia superficialis. At the points where the tendons of the feather muscles attach to a feather follicle, the Stratum profundum of the dermis is considerably compressed and merges with the connective tissue of the Stratum superficialis, which is part of the feather follicle. The fibers of the tendons of the feather muscle fiber bundles and their connective tissue envelope, mingle and merge with the Stratum compactum of the dermis of the feather follicle, thereby establishing a tight connection. The size and length of the individual feather muscles are directly correlated to the size of the individual feather follicles and the distance between them.

3.5.2. Apterial muscles (Mm. apteriales)

Apterial muscles consist of parallel fiber bundles that are enveloped and held together by a sheet of elastic connective tissue that bridges any gaps between them _quasi_ as the epimysium of the muscle and, therefore, forms a distinct layer that spans the apteria (see Figure 7). If the apteria bear semiplumes, the fiber bundles converge toward and attach to the feather follicles on their way across the apterium. These attachments are not shown in the diagrammatic Figure 7. The apterial muscles maintain a continuum with the feather muscles by attaching, via tendons, to the follicles of contour feathers along the periphery of feather tracts. Thus, the peripheral feather follicles of the pterylae serve as attachment points for apterial muscles as well as for feather muscles.

The connective tissue sheet enveloping the apterial fiber bundles and bridging the gaps between them is continuous with the connective tissue sheet enveloping the feather muscle fiber bundles and crossing the center of the parallelograms circumscribed by feather muscles. This can be especially well seen at the border between a feather tract and an apterium, where the peripheral feather follicles along the border are not directly interconnected by feather muscles. Because of this, the areas circumscribed by feather muscles along the border of a feather tract are in open connection with any gap between the apterial fiber bundles attaching to the peripheral feather follicles of a feather tract and are covered by a continuous connective tissue sheet.

The apterial muscles are named according to the apteria they underlie. There are no apterial muscles in the head region because there are no capital apteria.

Depending on the location, the fiber bundles vary in their thickness and density from being barely visible even under magnification to having the appearance of skeletal muscle (see Table 4). The fiber bundles themselves consist of alternating tendinous and muscular segments. If these segments are aligned across fiber bundles, the apterial muscles appear to consist of alternating transverse bands of muscle and connective tissue. In general, the length of the tendinous segments within a particular fiber bundle is less variable than the length of muscular segments (see Table 4). Depending on the region, the absolute and relative lengths of the tendinous and muscular segments of the fiber bundles vary. A single fiber bundle can change its tendon-muscle pattern as it crosses from one region to the other.

Based on the density and thickness of the fiber bundles and the relative and absolute lengths of the muscular and tendinous segments, certain structural patterns can be recognized (see Figure 7, Table 4). The cranial part of the M.apt. cervicalis lateralis, the caudal part of the M.apt. scapularis, and the M.apt. axillaris are thin, with widely spaced fiber bundles and relatively short muscle and tendon segments. The cranial part of the M.apt. truncalis is similar, except that its tendon segments are longer. The M.apt. sternalis is thin, of intermediate density, and has relatively short muscle and tendon segments. The caudal part of the M.apt. cervicalis lateralis and a transitional zone between the cranial and caudal part of the M.apt. truncalis are similar, except that they are thicker. The M.apt. pectoralis is special in that it is of intermediate thickness, high density, and has long muscle and short tendon segments. Finally, the cranial part of the M.apt. scapularis, the caudal part of the M.apt. truncalis, and the M.apt. cervicalis ventralis are the most strongly developed muscles, being thick, very dense, and having short muscle and tendon segments. These muscles have the appearance of skeletal musculature.

3.5.2.1. Apterial muscles of the neck

M. apterialis cervicalis lateralis: The M. apterialis cervicalis lateralis (M.apt.cel) extends across the entire length of the lateral cervical apterium and attaches to the peripheral feather follicles along the ventral border of the dorsal cervical feather tract and the dorsal borders of the occipital and ventral cervical feather tracts. From its cranial border between the occipital and dorsal cervical feather tracts to the level midway between the peduncle of the beard and the caudal end of the lateral cervical apterium, the M.apt.cel is very thin, its fiber bundles are widely spaced, and the muscle and tendon segments are relatively short (see Table 4). Therefore, the M.apt.cel is easily overlooked (e.g., Lucas and Stettenheim 1972). In its caudalmost part, the fiber bundles of the M.apt.cel become thicker, more closely spaced, but its muscle and tendon segments remain relatively short (see Table 4). Due to its thickness and increased density of the fiber bundles, the caudal part of the M.apt.cel is more easily identified as an apterial muscle than its cranial part (see Lucas and Stettenheim 1972).

M. apterialis cervicalis ventralis: The M. apterialis cervicalis ventralis (M.apt.cev) spans the ventral cervical apterium. It connects the peripheral feather follicles of the two contralateral ventral cervical feather tracts. At its caudolateral border along the palpable clavicle, its fiber bundles are continuous dorsally with those of the M.apt. pectoralis across the clavicle and assume its fiber bundle pattern. Most of its fiber bundles are thick, closely spaced, and the tendinous and muscular segments are relatively short. The M.apt.cev is, thus, similar in appearance to the cranial one third of the M. apterialis scapularis and to the caudal part of the M. apterialis truncalis. In its most caudoventral part, its fiber bundle arrangement is more similar to that of the M.apt. pectoralis, namely of intermediate thickness and high density and with long muscle and short tendon segments.

3.5.2.2. Apterial muscles of the thorax

M. apterialis scapularis: The M. apterialis scapularis (M.apt.sca) is the caudal extension of the M. apterialis cervicalis lateralis. It starts at the level of the shoulder joint and extends across the entire scapular apterium. Most of the M.apt.sca interconnects to the peripheral feather follicles of the interscapular and scapular feather tracts. In its caudalmost and transversal part, it interconnects the peripheral feather follicles along the medial border of the scapular feather tract to the peripheral feather follicles along the craniolateral border of the middorsal wedge of the dorsal feather tract, which projects cranially to the caudal end of the middorsal spinal apterium. It also attaches to the follicle of the caudalmost semiplume of the spinal apterium. In the cranial two thirds of the cranial one third of the M.apt.sca, the fiber bundles are thick and closely spaced with short muscle and tendon segments (see Table 4). This part of the M.apt.sca can easily be misidentified as skeletal musculature. In the caudal one third of its cranial one third, the M.apt. scapularis is of intermediate density and thickness with short muscle and tendon segments like the caudal part of the M.apt. cervicalis lateralis. In the caudal two thirds, the fiber bundles become thinner and more widely spaced with short tendinous and muscular segments similar to the pattern of the cranial part of the M.apt. cervicalis lateralis (see Table 4).

M. apterialis axillaris: The M. apterialis axillaris (M.apt.axi) spans the roughly pentagonal axillary apterium and extends diagonally from cranioventral to caudodorsal (see Figure 7). Cranially, the fiber bundles attach to the peripheral feather follicles of the ventral cervical feather tract and run dorsocaudally to attach to the peripheral feather follicles of the ventral border of the scapular feather tract, to the peripheral semiplume follicles of the prepatagial apterium (sensu Lucas and Stettenheim 1972), and to the peripheral follicles of the semiplumes of the subhumeral feather tract (sensu Lucas and Stettenheim 1972) on the base of the wing. Farther caudally, the fiber bundles attach to the peripheral feather follicles along the dorsal border of the pectoral feather tract and run dorsocaudally to attach to the peripheral feather follicles of the subhumeral and axillary feather tracts. The relatively straight parallel fiber bundles in the center of the muscle gradually assume a more curved orientation around the craniodorsal and caudoventral corners to connect the respective sides of these angles. The fiber bundles of the M.apt.axi are relatively thin, widely spaced, and short tendinous and muscular segments similar to the pattern of the cranial part of the M. apteriales cervicalis lateralis and the caudal part of the M. apterialis scapularis (see Table 4).

M. apterialis truncalis: The M. apterialis truncalis (M.apt.tru) extends across the trunk apterium, which has been studied only in its thoracic portion for this study. Cranially, a few fiber bundles attach to peripheral follicles of semiplumes along the ventral border of the caudal part of the posthumeral feather tract (sensu Lucas and Stettenheim 1972) on the base of the wing and curve cranioventrally and ventrally to attach to the peripheral feather follicles along the ventral half of the caudal border of the axillary feather tract and along the caudodorsal border of the caudal end of the pectoral feather tract. These fiber bundles are very thin and widely spaced with very short muscular segments and very long tendinous segments (see Table 4). Further caudally, the fiber bundles attach to the feather follicles along the ventral border of the dorsal feather tract and run ventrally to attach to the feather follicles along the caudodorsal border of the very end of the pectoral feather tract. Even further caudally, beyond the caudal end of the pectoral feather tract, the fiber bundles arising along the ventral border of the dorsal feather tract extend ventrally and are continuous with the fiber bundles of the M. apterialis pectoralis (see next). The fiber bundles are thick, very densely arranged with short tendinous and muscular segments (see Table 4). Therefore, this part of the M.apt.tru has a similar appearance to that of the cranial one third of the M. apterialis scapularis. The cranialmost, curving fiber bundles enclose a halfmoon-shaped connective tissue sheet between themselves and the dorsal half of the caudal border of the axillary feather tract. This halfmoon-shaped connective tissue sheet does not contain any fiber bundles and is part of the elastic fascia enveloping the entire smooth musculature of the skin.

M. apterialis pectoralis: The M. apterialis pectoralis (M.apt.pec) spans the pectoral apterium, which has been studied only in its thoracic portion for this study. Cranially, the fiber bundles attach to the peripheral feather follicles along the ventral border of the pectoral feather tract and run across the midventral line to attach to the feather follicles on the contralateral pectoral feather tract. Farther caudally, the fiber bundles arising from the feather follicles along the ventral and caudoventral borders of the pectoral feather tract attach to the peripheral feather follicles along the craniodorsal and dorsal borders of the sternal feather tract. Beyond the caudal end of the pectoral feather tract, the fiber bundles are dorsally continuous with those of the M. apterialis truncalis. Most of its fiber bundles are of intermediate thickness, are closely spaced, and have long muscular and short tendinous segments (see Table 4).

At its cranioventral border along the palpable clavicle, the fiber bundles are ventrally continuous with those of the M.apt. cervicalis ventralis and assume its fiber bundle pattern. Farther caudally, along the caudal half of the dorsal border of the sternal apterium, the fiber bundles are ventrally continuous with those of the M.apt. sternalis and assume its fiber bundle pattern (see Figure 7, Table 4). As the fiber bundles of the M.apt. sternalis are less densely arranged than those of the M.apt. pectoralis, some of the fiber bundles that attach to semiplumes along the ventral border of the pectoral apterium do not continue into the sternal apterium.

M. apterialis sternalis: The M. apterialis sternalis (M.apt.ste) spans the sternal apterium and for most of its part connects the peripheral feather follicles along the ventral border of the contralateral sternal feather tracts. Most of the fiber bundles are thin, intermediate in spacing, and with short tendinous and muscular segments (see Table 4). Along the ventral border of the pectoral apterium between the clavicle and the cranial tip of the sternal feather tract, the fiber bundles are dorsally continuous with those of the M.apt. pectoralis. The cranial half of these fiber bundles between the cranial tip of the sternal apterium and the apex of the sternal carina have the same muscle fiber pattern as those of the M. apterialis pectoralis (see Figure 7).

M. apterialis spinalis: The M. apterialis spinalis (M.apt.spn) is confined to the narrow, middorsal spinal apterium which bears a single row of semiplumes. It is not a sheet-like muscle like the rest of the apterial muscles, but resembles the bandlike feather muscles. It runs from one semiplume follicle to the other in the spinal apterium and interconnects the peripheral feather follicles along the medial borders of the contralateral interscapular feather tracts. At its caudal end, it connects the caudalmost follicle of a semiplume in the spinal apterium to the cranialmost feather follicle of the dorsal feather tract. At its cranial end, the M.apt.spn runs between the cranialmost follicle of a semiplume in the spinal apterium and the caudalmost middorsal feather follicle of the dorsal cervical feather tract.

3.6. Superficial fascia (Fascia superficialis)

The Fascia superficialis (F.supf) is a distinct layer of collagenous connective tissue that lies between the smooth dermal musculature (Stratum musculare viscerale) and the constrictor layer (Stratum constrictor; see 3.7). In birds, the Fascia superficialis was mentioned as a connective tissue layer first by Wiedemann (1802) and Kaupp (1918). Since then, however, it was generally termed "subcutis" and regarded as fat-rich, loose connective tissue (Moser 1906; Lange 1929, 1931; Lucas and Stettenheim 1972; Hodges 1974). The nature of the connection between the F.supf and the Stratum musculare viscerale varies from fusion to tight or loose attachment (see Figure 8). The F.supf is always interlarded with fat, but its thickness and, thereby, the amount of the interlarding fat varies. The fascia can be thin, thick, or of intermediate thickness depending on the region of the body (see Figure 9A). The variability of the F.supf correlates at least partly with the pterylography, with the distribution pattern of dermal fat in the Stratum profundum of the dermis, and with the presence of certain subcutaneous structures.

In addition to the fat that interlards the F.supf, fat is also present within distinct fat bodies (Corpora adiposa) which are anchored to the undersurface of the F.supf and are present in the head region and the region surrounding the base of the wing (see Figure 9B). Fat bodies are sandwiched between two delicate connective tissue laminae (Laminae externa et interna corporis adiposi fasciae superficialis) of a distinct deep fascial lamina (Lamina profunda fasciae superficialis), which separates from the underside of the main F.supf. The external lamina of the fat body and the underside of the main F.supf are connected only by very loose connective tissue. In this manner, the fat bodies remain anchored to the underside of the Fascia superficialis, while remaining able to move relative to it and, thereby, adjust to shifts of the skin. Connective tissue branching from both the external and internal laminae dips into the fat tissue and partitions it into smaller subunits. The fat tissue within these smaller units and within the fat body as a whole serves not only as a storage place for fat and energy (see Liebelt and Eastlick 1952, 1954; McGreal and Farner 1956; Feldman et al. 1962; King and Farner 1965; Blem 1976), but also have biomechanical functions as hydraulic cushions and filling material.

This study is the first to describe the Fascia superficialis as a distinct subcutaneous layer, as well as the microanatomy and exact location of the fat bodies (Corpora adiposa).

3.6.1. Connection between the F. superficialis and the Stratum musculare viscerale

The nature of interconnection between the thin elastic lamina of the Stratum musculare viscerale and the F. superficialis varies greatly depending on the region of the body (see Figure 8). The pattern of varying connections correlates at least partly with the pterylography, with the pattern of dermal fat distribution in the Stratum profundum of the dermis, with the pattern of varying connections between the F. superficialis and constrictor layer, and with certain subcutaneous structures. The F. superficialis is fused with the overlying Stratum musculare viscerale under the Apterium cervicale ventrale overlying the crop region and also for most of the neck and dorsal part of the thorax. The F. superficialis is also fused to the overlying cutaneous layer where it anchors along the edges of the nasal operculum, the root of the rhamphothecae, the eye, and the external ear opening. Over the head, there is a tight connection between the two layers, which extends to the gular region of the neck and in a concave curve to the dorsal side of the cranial part of the neck caudad up to the caudal border of the cranial part of the overlying dorsal cervical feather tract that is characterized by small feathers, no subepidermal fat pad, and a high density of feathers (see Figures 2 and 8). This region of tight connection is congruent with the region where the F. superficialis is of intermediate thickness (see Figure 9A).

A tight connection is also present in a small area underlying the lateral cervical apterium between two clearly defined borderlines (see Figure 9A). This area lies under the small overlying area of dermal fat with intermediate thickness (see Figure 5). Its cranial borderline lies at the same level as the borderline between the parts of the overlying M. apterialis cervicalis lateralis with low and intermediate densities of fiber bundles (see Figure 7) and as the cranial border of the underlying cervicoscapular fat body of the F. superficialis (see Figure 9B). The caudal borderline of the area with a tight connection coincides with the caudal border of the underlying M. constrictor (see Figure 11). Another area of tight connection between the F. superficialis and the Stratum musculare viscerale is found in an area underlying the caudal part of the scapular apterium (see Figure 8). The cranial border of this area coincides with the caudal border of the cervicoscapular fat body of the F. superficialis and the cranial border of the M. latissimus dorsi cranialis (sensu Vanden Berge 1975) (see Figure 9B). This area of tight connection also coincides with the overlying area of dermal fat of intermediate thickness (see Figure 5) and the area of tight connection between the F. superficialis and the constrictor layer (see Figure 10). The last two areas with a tight connection between the F. superficialis and the

Stratum musculare viscerale are found under the axillary and pectoral feather tracts and under the sternal apterium and feather tract (see Figure 8). No clear-cut correlation with overlying or underlying areas could be found for these areas.

A loose connection between the F. superficialis and the Stratum musculare viscerale does not occur under feather tracts. It is found, however, in the area underlying the trunk and pectoral apterium (see Figure 8). It is also found in an area underlying the caudalmost part of the lateral cervical apterium and the cranial part of the scapular apterium. The cranial border of this area coincides with the caudal border of the underlying M. constrictor (see Figure 11), whereas its caudal border coincides with that of the cervicoscapular fat body and the cranial border of the M. latissimus dorsi cranialis (sensu Vanden Berge 1975) (see Figure 9B). This area of loose connection coincides with the overlying area of thick dermal fat (see Figure 5) and of loose interconnection between the F. superficialis and the constrictor fascia (see Figure 10).

3.6.2. Thickness of the F. superficialis

The interlarded F. supf can be thick, thin, or of intermediate thickness depending on the region of the body. The pattern of varying thickness of the fascia correlates at least partly with the pterylography, with the pattern of dermal fat distribution in the Stratum profundum of the dermis, and with certain subcutaneous structures. Over the head, the fascia is of intermediate thickness, which extends to the gular region of the neck and in a concave curve to the dorsal side of the cranial part of the neck caudad up to the caudal border of the cranial part of the overlying dorsal cervical feather tract that is characterized by small feathers, no subepidermal fat pad, and a high density of feathers (see Figures 2, 8 and 9). The F. superficialis is thin in the area underlying the axillary apterium and in a large area of the neck (see Figure 9A). The latter area comprises the area caudal to that of the fascia with intermediate thickness on the cranial part of the neck, as well as the areas underlying the ventral cervical apterium, the lateral cervical apterium caudad to the level of the caudal border of the M. constrictor, and the part of the ventral cervical feather tract that is characterized by small feathers, no subepidermal fat pad, and a high density of feathers. The rest of the body, including the auricular feather tract, is covered by thick F. superficialis.

The ventral side of the F. superficialis consists of a layer of distinct parallel, longitudinal connective tissue fibers, the Lamina longitudinalis, where it underlies most of the dorsal cervical feather tract and the entire interscapular feather tract. The Lamina longitudinalis arises cranially roughly at the border between the dorsal raphe and caudal dorsal aponeurosis of the M. constrictor. The area of the Lamina longitudinalis coincides with the area of fusion between the F. superficialis and the Fascia constrictor (see Figure 10).

3.6.3. Fat bodies of the Fascia superficialis (Corpora adiposa fasciae superficialis)

3.6.3.1. Corpus adiposum faciale

The Corpus adiposum faciale (C.fac) is elongated and loop-shaped (see Figure 9B). It extends from the rictus to almost the ventral border of the external auditory meatus. The two arms of the loop enclose the underlying palpable jugal arch.

The fat tissue is contained between the Lamina externa et interna fasciae superficialis corporis adiposi facialis, which split from the deep lamina of the F. superficialis. The deep lamina separates from, but remains anchored to the underside of the main F. superficialis which is fused to the constrictor fascia in this region (see Figure 10). The C.fac has a cushioning function as the jugal arch of the turkey (Meleagris) bows outward (see Shufeldt 1887, 1914) and projects under the skin, unlike that of other genera of Galliformes.

3.6.3.2. Corpus adiposum cervicoscapulare

The Corpus adiposum cervicoscapulare (C.csca) underlies the caudalmost part of the lateral cervical apterium and the cranial portion of the scapular apterium. Its cranial border lies cranial to the caudal border of the M. constrictor and coincides with the borderline between the parts of the overlying M. apterialis cervicalis lateralis with low and intermediate density of their fiber bundles (see Figures 7 and 9B). The caudal border of the cervicoscapular fat body coincides with the cranial border of the M. latissimus dorsi cranialis (sensu Vanden Berge 1975), which lies under the constrictor layer. The medial (i.e., dorsal) border of the fat body flanks the cranial part of the ventral border of the underlying M. subcutaneous dorsalis, which lies slightly lateral to the lateral border of the interscapular feather tract. The lateral border of the fat body starts cranially by following the dorsal border of the overlying ventral cervical feather tract and the dorsal edge of the caudo-dorsal process of the Corpus adiposum supraingluviale of the underlying constrictor layer. Cranial to the prepatagial part of the base of the wing, the medial border of the fat body is indented to turn dorsally around a prominent bulge of the underlying M. rhomboideus superficialis (sensu Vanden Berge 1975). But near the cranial end of the base of the wing, the fat body expands again laterally so that it underlies the scapular feather tract as well as the scapular apterium. The area of the cervicoscapular fat body, which underlies parts of the lateral cervical and scapular apteria, coincides with the area of loose connection between the F. superficialis and constriction layer (see Figure 10).

The fat tissue is contained within the Laminae externa et interna fasciae superficialis corporis adiposi cervicoscapularis, which split from the deep lamina of the F. superficialis. This deep lamina separates from, but remains anchored to the underside of the main F. superficialis. The C.csca functions as a cushion to fill the depressed area under the scapular apterium between the caudal border of the M. constrictor and the cranial border of the M. latissimus dorsi cranialis (sensu Vanden Berge 1975).

3.6.3.3. Corpus adiposum supraalare

The Corpus adiposum supraalare (C.spal) is located in the thorax dorsal to the caudal end of the base of the wing. It is triangular and fills the depressed region bordered by bulging underlying muscles. Its cranial edge is flanked by the caudal border of the underlying skeletal M. latissimus dorsi cranialis (sensu Vanden Berge 1975); its dorsal edge is flanked by the lateral border of the M. subcutaneus dorsalis of the underlying constrictor layer (see 3.7.1.2); and its caudoventral edge is flanked by the craniodorsal border of the M. subcutaneus dorsoalaris of the underlying constrictor layer (see 3.7.1.3; Figure 9B).

The fat tissue is contained within the Laminae externa et interna fasciae superficialis corporis adiposi supraalaris, which split from the deep lamina of the F. superficialis. This deep lamina separates from, but remains anchored to the underside of the main F. superficialis. The fat body serves mainly as a filling material.

3.6.3.4. Corpus adiposum retroalare

The triangular Corpus adiposum retroalare (C.ral) is located in the thorax caudal to the base of the wing (see Figure 9B). It is confined to a depressed region between two bulging subcutaneous muscles of the constrictor layer. Its craniodorsal edge is flanked by the caudoventral border of the M. subcutaneus dorsoalaris, and its cranioventral edge is flanked by the caudodorsal border of the thoracic part of the M. subcutaneus abdominoalaris.

The fat tissue is contained between the Laminae externa et interna fasciae superficialis corporis adiposi retroalaris, which split from the deep lamina of the F. superficialis. This deep lamina separates from, but remains anchored to the underside of the main F. superficialis. The fat body serves mainly as a filling material.

3.6.3.5. Corpus adiposum subalare

The Corpus adiposum subalare (C.sbal) is located in the thorax ventral and caudal to the base of the wing. Its narrow cranial limb hugs the ventral side of the base of the wing, except its prepatagial part (see Figure 9B). The caudal part is wide and roughly rectangular. It occupies the depressed retropectoral region (see Figure 1), where it forms a thick cushion. The caudodorsal edge of the C.sbal is flanked by the cranioventral border of the thoracic part of the M. subcutaneus abdominoalaris of the underlying constrictor layer (see 3.7.1.6.), and its cranial border is flanked by the caudal border of the M. subcutaneus thoracoalaris of the underlying constrictor layer.

The fat tissue is contained within the Laminae externa et interna fasciae superficialis corporis adiposi subalaris, which split from the deep lamina of the F. superficialis. This deep lamina separates from, but remains anchored to the underside of the main F. superficialis. The fat body serves mainly as a cushioning material to fill the axillary depression and the depression caudal to the base of the wing.

3.7. Constrictor layer (Stratum constrictor)

The constrictor layer is a distinct layer of connective tissue which incorporates skeletal muscles and fat bodies (Corpora adiposa). It is named after the cervical M. constrictor (see Table 5 for synonymies), the best known muscle of this layer. The constrictor layer lies deep to the F. superficialis (see 3.6.). Previously, this layer has not been recognized as such and, therefore, has not been studied in its entirety. The muscles of the constrictor layer are subcutaneous muscles and have no attachments to any bony elements of the skeleton.

The nature of interconnections between the constrictor layer and the overlying F. superficialis varies (Figure 10). Even though a distinct pattern of areas with fused, tight or loose connections emerges and even though some borderlines of these areas coincide with those of overlying areas, no consistent correlations can be established between the nature of connection between the constrictor layer and the F. superficialis on the one hand and the specific characteristics of any of the overlying layers on the other hand. It is possible that the observed patterns of interconnections are actually correlated to some underlying structures that have not been studied in the present context, or to some localized functional demands that may become apparent only as future studies will proceed to incorporate deeper layers of the body and its appendages.

Although muscles and fat bodies are part of the constrictor layer, most of this layer actually consists of a distinct connective tissue layer which may be either an aponeurosis, if it is an extension of subcutaneous muscle fiber bundles via myotendinous junctions, or a fascia, if it attaches along the borders of subcutaneous muscles or covers vast stretches of the body surface (see Figure 11). More specifically, fasciae attach to the epimysia enveloping the subcutaneous muscles and to the epitenonia enveloping their aponeuroses. Because the connective tissue of the aponeuroses and fasciae smoothly intergrade from one to the other, the distinction between aponeuroses and fasciae is based more on functional than on structural criteria. This distinction, however, is not a purely academic one since the aponeuroses insert to particular structures and, therefore, determine the functions of the subcutaneous muscles, whereas the fasciae serve mainly to maintain the integrity of the constrictor layer.

The striated subcutaneous muscles of the constrictor layer have variously been referred to as dermal muscles (Shufeldt 1890, Fisher 1955, Osborne 1968, Lucas and Stettenheim 1972, Starck 1982), as cutaneous muscles (Bradley 1951, Fitzgerald 1969, Hodges 1974), and as being part of the superficial neck muscles (Homberger and Meyers 1989). Based on the observations made in the present study, and to avoid further confusion, this group of muscles is now referred to as the subcutaneous muscles of the constrictor layer.

The subcutaneous muscles can be classified basically into four categories depending on the sites of their attachments. First, the aponeuroses of subcutaneous muscles may simply become part of the connective tissue of the constrictor layer without attaching to the overlying layers by remaining only loosely or tightly attached to, but not fusing with them (e.g., the cranial two thirds of the M. constrictor; compare Figures 10 and 11). Second, the aponeuroses of certain parts of the subcutaneous muscles (i.e., partes dermis) may fuse with the overlying Fascia superficialis and, thereby, indirectly with the cutis (e.g., pars dermis of the M. constrictor and Mm. subcutanei thoracoalaris, abdominoalaris et dorsoalaris; compare Figures 8, 10, and 11). Third, tendons of individual superficial fascicles of some subcutaneous muscles (i.e., partes pennarum) attach to feather follicles on the periphery of feather tracts that are characterized by large feathers, a subepidermal fat pad, and a high density of feathers (e.g., pars pennarum of the M. constrictor and Mm. subcutanei thoracoalaris et thoracoabdominalis; see Figures 11 and 12). Fourth, the aponeuroses of certain parts of subcutaneous muscles may attach to fat bodies of the constrictor layer (e.g., pars supraingluvialis of the M. constrictor; see Figure 11).

The role of the subcutaneous muscles of the constrictor layer has until now remained an enigma in avian anatomy. Shufeldt (1890) observed that subcutaneous muscles completely avoid apteria, and Petry (1951) specifically named them "muscles of the feather tracts" and mentioned that there are "tendinous junctions between striated and smooth muscles." Boas (1931) considered them to be usually connected to the skin of pterylae and to raise feathers when they contract. Bradley (1951) said that they cause the erection of feathers. Osborne (1968), after histological examination of teased subcutaneous muscles at their "insertion end", concluded that they do not attach to feather follicles but instead attach by fascia to the undersurface of the skin. Vanden Berge and Zweers (1993) concluded that the subcutaneous muscles attach to the "innermost lamina" of feather tracts and not to individual feather follicles. As can be easily recognized now, the reason for the confusion and lack of understanding of the function of the subcutaneous muscles lay in the incomplete and inaccurate anatomical descriptions of these muscles. As the attachment sites of the various subcutaneous muscles and their parts have been clearly established in this study, the functions of the individual muscles become apparent. The subcutaneous muscles that attach to and exert a pull on the Fascia constrictor itself serve mainly to tighten the fascia. The partes dermis of the subcutaneous muscles serve to tighten or readjust the position of the skin after it was passively stretched. The partes pennarum serve to move entire feather tracts. Their attachments to feather follicles do not serve to move individual feathers because their muscle fiber direction differs from that of the smooth feather muscles and the main plane of motion of the feathers. Furthermore, the partes pennarum do not attach directly to the dermal feather follicles, but indirectly to them at sites where the Fascia superficialis is fused to the feather follicles (see Figure 6). Finally, the parts of the subcutaneous muscles that attach to fat bodies use the fat bodies as non-expandable and cushioning shields to exert pressure on underlying structures, such as the pars supraingluvialis of the M. constrictor does on the crop.

The fat bodies of the constrictor layer (Corpora adiposa fasciae constrictoris), unlike those of the Fascia superficialis, are built into the constrictor fascia itself and not attached to the underside of the fascia (compare with 3.6.3.). The fascia constrictor itself simply splits into an external and an internal lamina (Laminae externa et interna corporis adiposi fasciae constrictoris), and the fat tissue is sandwiched between the two laminae. The location of fat bodies of the constrictor layer correlates with the presence of underlying structures, and, at least in two cases, they serve to provide extra padding and cushioning.

3.7.1. Muscles of the constrictor layer (Musculi strati constrictoris)

3.7.1.1. M. constrictor

The M. constrictor (M.c) is a sheet-like muscle that encircles the neck in a sleeve-like fashion (see Figure 11; Table 5). The contralateral halves of the muscle meet along the dorsal and ventral midlines through raphae or through aponeuroses that may constitute a major part of the muscle (see Figure 11). The cranial border of the M. constrictor lies just caudal to the external ear opening and curves dorsad just slightly beyond the external ear opening, with the convex side of the curvature facing cranially (see Figure 11). Dorsally, it continues as an aponeurosis that covers the occipital region of the head and is only loosely attached to the overlying Fascia superficialis (see Figure 10). The cranial border of the M. constrictor is anchored cranially to the overlying F. superficialis by the short, halfmoon-shaped Fascia constrictor cranialis (F.c.cran) which fuses with the F. superficialis (see Figure 10). The caudal border of the M. constrictor is also curved, but the concave side of the curvature faces caudally so that the middle of the curvature lies at the level of the center of the caudalmost section of the M. apterialis cervicalis lateralis (see Figures 7 and 11). This level also coincides with the borderline between the thin and thick parts of the overlying F. superficialis (see Figure 9A). The caudoventral end of the caudal border of the M. constrictor, however, reaches the level of the borderlines between the overlying lateral cervical and scapular apteria (see Figure 11). The entire caudal border is overlaid by the Corpus adiposum cervicoscapulare of the F. superficialis, which reaches cranially the borderline between the parts with low and intermediate density of the M. apterialis cervicalis lateralis (see Figure 7). The Fascia constrictor caudalis (F.c.caud) extends caudad from the caudal border of the M. constrictor and continues as the constrictor fascia of the thorax.

The density of the muscle fiber bundles of the muscular part and the relative length of the muscular and aponeurotic portions of the M. constrictor change across its width over the length of the neck. For descriptive purposes, the M. constrictor can be divided into roughly two halves: The cranial half is mostly muscular with a compact muscle fiber arrangement, and the caudal half has long dorsal and ventral aponeuroses that together roughly equal the length of the muscular part (see Figure 11). The borderline between these two halves lies roughly at the level of the apex of the ventrally convex curvature of the skeletomuscular part of the neck. The cranial half is the part of the M. constrictor that has been most often, if at all, observed by previous anatomists. Caudad from this compact muscle portion up to the level of the cranial border of the peduncle of the beard, the muscle fiber bundles are arranged less densely. The epimysium appears here as thin connective tissue sheets between the individual muscle fiber bundles. This part of the M. constrictor is difficult to dissect even under high magnification, not only because of the reduced density and length of the muscle fiber bundles, but also because of their mostly tight attachments to the overlying F. superficialis and the fusion of their aponeuroses with the overlying F. superficialis (see Figure 10). Thus, it is easily understandable why this part of the M. constrictor has not been described previously. As a consequence, the caudal part of the M. constrictor caudad to the level of the peduncle of the beard, although it regains the compactness observed in the cranial half of the M. constrictor, has been misinterpreted as a muscle different from the M. constrictor as it appears to blend with the M. cucullaris complex (sensu Vanden Berge 1975), which actually lies under the constrictor layer.

The extent of the raphae and dorsal and ventral aponeuroses varies across the length of the neck. Middorsally, the cranialmost muscle fiber bundles become aponeurotic just dorsal to the external ear opening. Therefore, there is a cranial dorsal aponeurosis as a relatively wide middorsal connective tissue sheet. It gradually narrows caudad, and at the level of the cranial border of the cervical caruncles, it has become a middorsal raphe. The raphe, however, is often obscured, because most of the superficial muscle fiber bundles cross over the middorsal line to the contralateral side. The raphe extends caudad to the level of the caudal border of the cervical caruncles. This point is also the cranial origin of the Lamina longitudinalis of the overlying F. superficialis (see 3.6.). At this point, the dorsal raphe widens rapidly into an aponeurosis so that the borderline between the dorsal aponeurosis and the muscular part of the M. constrictor (i.e., the level of myotendinous junctions) coincides with the borderline between the dorsal cervical feather tract and the lateral cervical apterium. The dorsal aponeurosis reaches its final length, which it maintains to the caudal border of the muscle, at roughly midwidth of the M. constrictor, which coincides with the caudal border of the compact muscular cranial portion of the M. constrictor and with the cranial border of the wide ventral aponeurosis of the M. constrictor. This point also coincides with the cranial end of an underlying middorsal fat body.

On the ventral side of the M. constrictor, a midventral raphe starts cranially and extends caudad all the way to the end of the compact portion of the muscle, where the ventral aponeurosis starts. Midway between the cranial border of the muscle and the overlying cervical caruncles, some superficial muscle fibers start to criss-cross over the raphe. The ventral aponeurosis starts cranially at mid width of the M. constrictor. As it extends caudad, it fuses with the overlying F. superficialis along the midventral line and along the border of the part of the overlying ventral cervical feather tract that is characterized by large feathers, a subepidermal fat pad, and a high density of feathers (see Figure 10). It remains fused with the F. superficialis all the way to the dorsal border of the overlying ventral cervical apterium and to the cranial border of the supraingluvial fat body of the constrictor layer, where it divides into the Laminae externa et interna enclosing the fat body.

The caudal one third of the M. constrictor lies dorsal to the part of the overlying ventral cervical feather tract that is characterized by large feathers, a subepidermal fat pad, and a high density of feathers. In this region, the M. constrictor consists of three parts: the pars pennarum, the pars dermis, and the pars supraingluvialis (see Figures 11, 12 and 13). The M. constrictor pars pennarum (M.c.penn) is the most superficial muscle part. It starts cranially at the level of the steplike broadening of the part of the ventral cervical feather tract that is characterized by large feathers, a subepidermal fat pad, and a high density of feathers, and extends caudad to a level slightly caudal to the borderline between the parts of the M. apterialis cervicalis lateralis with low and intermediate density of fiber bundles (see Figure 13). The individual muscle fascicles attach to feather follicles at varying distances from the dorsal border of the ventral cervical tract (see Figures 11 and 13). The M. constrictor pars dermis (M.c.derm) lies deep to the pars pennarum. It starts cranially at the level of the cranial end of the part of the ventral cervical feather tract that is characterized by large feathers, a subepidermal fat pad, and a high density of feathers, and extends caudad slightly cranial the caudal border of the pars pennarum (see Figures 11 and 13). As the caudal muscle fiber bundles curve caudoventrally, their ventral ends reach the caudal border of the pars pennarum. The attachment of the aponeurosis of the pars dermis to the F. superficialis more or less follows the distal side of the periphery of the attachments of the pars pennarum (see Figure 11).

The M.constrictor pars supraingluvialis (M.c.singl) is the deepest part. It starts cranially slightly cranial to the caudal end of the pars pennarum and extends caudad to the caudal border of the muscle (see Figures 11 and 13). It inserts along the entire width of the Corpus adiposum supraingluviale via a very short aponeurosis of about one millimeter or less.

The roles of the M. constrictor change with the structure across the entire length of the neck. In its cranial half, and especially in the gular region, the M. constrictor acts as a constrictor and an antagonist to expanding movements related to swallowing, lowering of the hyoid and larynx, and neck movements. In the caudal part, of the M. constrictor the pars dermis and pars pennarum exert a dorsal pull on the ventral cervical feather tract to reposition it (see Figures 4 and 13). They act as synergists to the M. apterialis cervicalis lateralis, and as antagonists to the diagonal feather muscles of the ventral cervical feather tract. The pars supraingluvialis assists in the suspension of the crop, especially when it is expanded, and in the compression of the emptying crop.

3.7.1.2. M. subcutaneus dorsalis

The M. subcutaneus dorsalis (M.sb.dor) is a thin, longitudinal, band-like muscle in the thorax. Its muscular part extends from a level slightly cranial to the midlength of the overlying interscapular feather tract to almost the caudal end of the thoracic part of the overlying dorsal feather tract. Its medial and lateral borders are shifted laterally relative to the medial and lateral borders of the overlying interscapular feather tract. The lateral border of the M.sb.dor is flanked by the dorsal border of the cervicoscapular fat body of the F. superficialis, except where it passes over the bulging underlying M. latissimus dorsi cranialis (sensu Vanden Berge 1975) (see Figure 9B). The muscle fiber bundles become aponeurotic at both the cranial and caudal ends. The tendon fiber bundles of the cranial end are distinct before they extend into and merge with the constrictor fascia slightly caudal to the cranial tip of the base of the wing (see Figure 11). The tendon fiber bundles of the caudal end are also distinct before they extend into and merge with the constrictor fascia. Unfortunately, the extreme caudal end of the tendon fiber bundles extend onto the trunk and could not be observed. Most of the M.sb.dor and its cranial end merges with the overlying F. superficialis via its epimysium and the Fascia constrictor. Its caudal end, however, is only tightly attached to the F. superficialis (see Figures 10 and 11).

Upon contraction, the M. subcutaneous dorsalis exerts a caudal pull on the constrictor fascia and the dorsal aponeurosis of the M. constrictor, which are fused to the overlying F. superficialis and skin (see Figures 8, 9 and 10). It probably also exerts a cranial pull on the F. superficialis which is fused to the cutis underlying the thoracic part of the dorsal feather tract. Thus, the M. subcutaneus dorsalis can readjust the position of all cutaneous and subcutaneous layers together by pulling on them after they may have shifted cranially in the course of neck movements or caudally in the course of trunk movements (compare Figures 8, 10 and 11).

### 3.7.1.3. M. subcutaneus dorsoalaris

The M. subcutaneus dorsoalaris (M.sb.doral) is a relatively short, diagonally oriented, band-like muscle in the thorax which runs parallel, but slightly caudal to the craniodorsal border of the overlying dorsal feather tract. The M.sb.doral arises caudodorsally from the surface of the connective tissue enveloping the underlying M. latissimus dorsalis caudalis (sensu Vanden Berge 1975) adjacent to the caudal end of the M. subcutaneous dorsalis. The M.sb.doral at first follows the ventral border of the M. subcutaneus dorsalis before it curves ventrally. As its cranioventral end reaches the craniodorsal end of the M. subcutaneus abdominoalaris, its muscle fiber bundles split into several layers that cross among the aponeurotic fiber bundles of the M. subcutaneus abdominoalaris, so that the fiber bundles of the two muscles are in effect interdigitating. After crossing the M. subcutaneus abdominoalaris, the muscle fiber bundles become aponeurotic. The most superficial aponeurosis becomes a pars dermis and attaches tightly to the overlying F. superficialis and, thereby, fuses with the dermis underlying the part of the scapular feather tract that extends onto the wing (not visible in Figure 11). The deeper muscle fiber bundles all become aponeurotic after the crossing and become part of the constrictor fascia extending onto the wing. The craniodorsal border of the M.sb.doral is flanked by the supraalar fat body of the F. superficialis, whereas the caudoventral border is flanked by the retroalar fat body of the F. superficialis (see Figure 9B).

The M.sb.doral, together with M. subcutaneus abdominoalaris (see next), exerts a caudal pull on the scapular feather tract which tends to slide cranially with the upward and forward movements of the wing during flight.

3.7.1.4. M. subcutaneus abdominoalaris

The M. subcutaneus abdominoalaris (M.sb.abdal) is a thick, diagonally oriented, band-like muscle in the thorax. It underlies and follows the cranioventral border of the overlying dorsal feather tract. As the craniodorsal end of the M.sb.abdal reaches the caudoventral border of the M. subcutaneus dorsoalaris, it becomes aponeurotic and splits in to several layers of aponeurotic fascicles among which the muscle fiber bundles of the M. subcutaneus dorsoalaris cross. The most superficial aponeurosis passes over the M. subcutaneus dorsoalaris and becomes a pars dermis by attaching tightly to the overlying F. superficialis and, thereby, fuses with the dermis underlying the caudal part of the scapular feather tract (see Figures 10 and 11). The deeper aponeurotic fascicles become part of the constrictor fascia after crossing the M. subcutaneus dorsoalaris. The caudodorsal border of the M.sb.abdal is flanked by the retroalar fat body of the overlying F. superficialis, whereas the cranioventral border is flanked, at least near its craniodorsal end, by the subalar fat body of the F. superficialis (see Figure 9A).

The M.sb.abdal, together with the M. subcutaneous dorsoalaris (see above), exerts a caudal pull on the scapular feather tract which tends to slide cranially with the upward and forward movements of the wing during flight.

### 3.7.1.5. M. subcutaneus thoracoalaris

The M. subcutaneus thoracoalaris is a thin sheet-like, fan-shaped muscle in the thorax. It underlies roughly the area of the axillary feather tract (see Figure 11). It arises from the constrictor fascia which dips deeply into the axillary depression at the base of the wing between the overlying axillary feather tract and the posthumeral feather tract of the wing (sensu Lucas and Stettenheim 1972). Its muscle fiber bundles fan out as they extend ventrad towards the dorsal border of the caudal half of the overlying pectoral feather tract. Most of the dorsal part of the cranial border of M.sb.thoral lies slightly caudal to the cranial border of the overlying axillary feather tract, and most of its caudal border lies slightly caudal to the caudal border of the axillary feather tract and spreads under the cranial part of the trunk apterium. The ventral half of the caudal muscle border is flanked by the subalar fat body of the overlying F. superficialis (see Figure 9B). The cranialmost muscle fiber bundles of M.sb.thoral curve cranially and, after becoming aponeurotic, merge with the connective tissue of the constrictor layer. The rest of the muscle fiber bundles can be subdivided into two portions. The cranial portion represents the pars dermis which attaches tightly to the overlying F. superficialis and, thereby, to the cutis (see Figures 8, 10 and 11). The caudal portion of muscle fiber bundles represents the pars pennarum and inserts on the peripheral feather follicles of the caudodorsal part of the pectoral tract which is characterized by large feathers, a subepidermal fat pad, and a high density of feathers (see Figure 11).

The partes dermis et pennarum of the M.sb.thoral exert a dorsal pull on the caudal half of the pectoral feather tract and, thereby, help to reposition it after it was displaced in the course of flight movements. Cranially and caudally to the M.sb.thoral, the M. apterialis axillaris and the cranial part of M. apterialis truncalis exert a caudodorsal and dorsal pull, respectively, on the pectoral feather tract (see Figure 7). Thus, the subcutaneous and apterial muscles inserting on the dorsal edge of the overlying pectoral feather tract form a muscle complex exerting a dorsal pull on this pteryla. In essence, the M.sb.thoral compensates for the lack of apterial musculature in the region overlaid by the axillary feather tract.

3.7.1.6. M. subcutaneus thoracoabdominalis

The M. subcutaneus thoracoabdominalis (M.sb.thoabd) is a thin, diagonally oriented, sheet-like muscle in the thorax. Cranially, the width of the muscle corresponds to the width of the caudal end of the pectoral feather tract, but the muscle widens as it extends caudad onto the abdomen (not visible in Figure 11). The muscle fiber bundles of the ventral one fourth of the muscle represent the pars dermis and attach tightly onto the overlying F. superficialis and, thereby, to the cutis (see Figures 8, 10 and 11). The muscle fiber bundles of the dorsal three fourths represent the pars pennarum and insert on some of the peripheral feather follicles of the caudalmost part of the pectoral feather tract which is characterized by large feathers, a subepidermal fat pad, and a high density of feathers (see Figures 4 and 11).

Upon contraction, the partes dermis et pennarum of the M.sb.thoabd exert a caudoventral pull on the overlying pectoral feather tract and can adjust its position.

### 3.7.2. The fat bodies of the constrictor layer (Corpora adiposa fasciae constrictoris)

#### 3.7.2.1. Corpus adiposum supraingluviale

The Corpus adiposum supraingluviale (C.singl) is unpaired and underlies a large area on the lateral and ventral sides of the base of the neck. Medially, it underlies the caudal two thirds of the ventral cervical apterium and extends dorsally under the caudal part of the ventral cervical feather tract up to close to the inserting end of the pars supraingluvialis of the M. constrictor (see Figure 11). Its caudal border follows the cranial border of the pars thoracis of the M. pectoralis (sensu Vanden Berge 1975). Dorsocaudally, the fat body forms a dorsal process that fills the area bordered by the caudal border of the M. constrictor, the ventral border of the Corpus adiposum of the overlying F. superficialis, the bulging part of the M. rhomboideus pars cranialis (sensu Vanden Berge 1975) in front of the prepatagial part of the base of the wing, and the cranial border of the thoracic part of the pectoral muscle (see Figures 9B and 11).

The fat tissue is contained between the Laminae externa et interna fasciae constrictoris corporis adiposi supraingluvialis. The Lamina externa is tightly connected to the overlying F. superficialis (see Figure 10). The dorsal border of the fat body is connected directly to the muscle fiber bundles of the pars supraingluvialis of the M. constrictor via an extremely short aponeurosis. It is this aponeurosis which splits into the external and internal laminae containing the fat body. Thus, the fat body forms a sling supporting most of the crop. Upon contraction of the pars ingluvialis of the M. constrictor, the fat body can be used to compress the crop, especially when it is emptying. The C.singl also probably has a protective function as it provides a cushion between the skin and the delicate wall of the crop, especially when it is expanded and full of seeds and other hard items.

3.7.2.2. Corpus adiposum axillare

The Corpus adiposum axillare (C.axi) is located on the lateral aspect of the thorax in the center of the overlying axillary apterium. It lies ventral to the shoulder joint and slightly caudal to the level of the clavicle. It is roughly heartshaped with the base pointing ventrally and the apex pointing dorsally towards the base of the wing (see Figure 11). The C.axi hugs the dorsal border of a palpable bulging part of the underlying M. pectoralis pars thoracis (sensu Vanden Berge 1975; see also Komarek et al. 1986). The fat tissue is contained between the Laminae externa et interna fasciae constrictoris corporis adiposi axillaris, which split from the Fascia constrictor. The Lamina externa has a tight connection with the overlying F. superficialis (see Figure 10). The function of the C.axi is unclear and may be related to underlying structures.

3.7.2.3. Corpus adiposum thoracale

The Corpus adiposum thoracale (C.thor) is sausage-shaped and located in the thorax under the ventral half of the caudal three fourths of the overlying pectoral feather tract.

The fat is contained between the Laminae externa et interna fasciae constrictoris corporis adiposi thoracalis, which split from the Fascia constrictor. The Lamina externa has a loose connection with the overlying F. superficialis (see Figure

10). The function of the C.thor is unclear and may be related to some underlying structures.

3.7.2.4. Corpus adiposum carinae

The unpaired midventral Corpus adiposum carinae (C.car) is narrow and elongated, and overlies the underlying keel of the sternum. It starts cranially slightly cranial to the apex of the keel and extends caudally to the level of about three fourths of the thoracic part of the sternal feather tract (see Figure 11). The fat tissue is contained between the Laminae externa et interna fasciae constrictoris corporis adiposi carinae, which split from the constrictor fascia. The Lamina externa is loosely connected to the overlying F. superficialis (see Figure 10). The C.car has mainly a protective function as it provides a hydraulic cushion between the bony keel of the sternum and the skin.

# CHAPTER 4: DISCUSSION

The present study on the functional anatomy of the integument and subcutaneous structures of the domestic turkey reveals two major points: 1) the interaction between the smooth apterial muscles (of the Stratum musculare viscerale) and the striated subcutaneous muscles (of the constrictor layer) in moving particular feather tracts, and 2) the deposition of fat in different cutaneous and subcutaneous layers and structures for energy storage and biomechanical purposes.

## 4.1. Interactions between smooth apterial and striated subcutaneous muscles.

A review of the literature on the smooth apterial and striated subcutaneous muscles reveals a plethora of contradictory statements about their anatomy and function.

Of the many confusions concerning the striated subcutaneous muscles, the most common one is related to the notion that they erect and depress the feathers (e.g., Barkow 1829, Helm 1886, Moser 1906, Boas 1931, Bradley 1951, Nickel et al. 1977, Starck 1982). However, since the muscle fiber bundles of the striated subcutaneous are not oriented in the direction of feather movements, they cannot perform this function (see Figure 6). Instead, the feather follicles serve as anchorage for the striated subcutaneous muscle fiber bundles which, upon contraction, exert a pull on entire feather tracts (see later). In contrast, Vanden Berge and Zweers (1993) reported that the striated muscles never attach to feather follicles. They based their report most likely on the study by Osborne (1968) on the skin muscles of the Phasianinae (i.e., pheasants and chickens), which concluded that "skin muscles" never insert on individual feather follicles. From the present study on the turkey, however, it is now apparent that these observations may have been made only on the striated subcutaneous muscles that do not comprise a pars pennarum and, therefore, do not attach to feather follicles.

The information on the smooth apterial muscle used to be very limited as they vary greatly in their thickness, density, and the relative length of the muscular and tendinous parts of their fiber bundles (see Figure 7, Table 4). Previous descriptions are based on the histology and some macroanatomy of the more obvious thick and dense apterial muscles (see Osborne 1968, Lucas and Stettenheim 1972). Petry (1951), not realizing that the elastic membrane and Fascia superficialis separate the smooth musculature (Stratum musculare viscerale) from the striated subcutaneous muscles, commented that these two types of muscles were sometimes interconnected through tendons. It is now apparent from the present study that Petry (1951) may have made these conclusions based on observations of apterial muscles that overlie an aponeurosis of a striated subcutaneous muscle at a point where the tendinous sections of apterial muscles were adhering to the underlying aponeurosis. Greschik (1915) thought that the well developed muscle network in the skin contained muscle fibers that were intermediate between the smooth and striated types. This idea, however, has been proven to be false by subsequent studies.

Based on the present study, it can be concluded that the smooth apterial and striated subcutaneous muscles complement each other in moving particular feather tracts. There are two excellent examples of this interaction: One in the neck where the M. apterialis cervicalis lateralis and the M. constrictor exert a dorsal pull on the ventral cervical feather tract, and another one in the thorax where the M. apterialis axillaris, the cranial portion of the M. apterialis truncalis, and the M. subcutaneus thoracoalaris exert a dorsal pull on the pectoral feather tract. In the neck, the skin is stretched in the longitudinal direction during various neck movements (Figure 4B; see also Osborne 1968). During these passive movements of the skin, the feather muscles remain unaffected because they are oriented diagonally to the main direction of the skin movement. Because of this arrangement, only the angles enclosed by the feather muscles, but not the distances between the feather follicles change when the skin is stretched. This means that the feather muscles that interconnect the feather follicles will not be stretched every time the neck is stretched, and that these muscles are able to move the feathers irrespective of skin movements. Although Osborne (1968) observed that the skin movements and the feather movements are decoupled and can occur independently from each other, he had no explanation for this phenomenon.

However, this structural configuration solves only part of the problem. As indicated in Figure 4B, when the skin is stretched longitudinally during neck movements, it also becomes narrower. In order for the skin to return to its original configuration, there must be some kind of a transversal force. That such a transversal force is necessary can also be seen in photographs of the Wild Turkey (see Timmer no date, Powell 1965) in which the dorsal and ventral cervical tracts are separated by a thin groove over the lateral cervical apterium and apparently need to be pulled together. The present study shows that this transversal force is provided by both the M.apterialis cervicalis lateralis and the partes pennarum et dermis of the M. constrictor (see Figures 11, 12 and 13). The transversal force exerted by the cranial part of the M. apterialis cervicalis lateralis with loosely arranged thin fiber bundles appears to be sufficient to pull the cranial part of the ventral cervical feather tract that is characterized by small feathers, no subepidermal fat pad, and a high density of feathers. But it is apparently not sufficient to pull the caudal part of the ventral cervical feather tract that is characterized by large feathers, a subepidermal fat pad, and a high density of feathers. Interestingly enough, along the dorsal periphery of this caudal part of the ventral cervical feather tract, the pars pennarum of the M. constrictor sends some superficial muscle fiber bundles to insert on some of the large feather follicles and the pars dermis of the M. constrictor fuses with the overlying F. superficialis, which is fused to the overlying cutis, to provide the needed additional force to pull the entire ventral cervical feather tract dorsally (see Figures 8, 10, 11, 12 and 13). The caudalmost part of the M. apterialis cervicalis lateralis, which overlies the caudal border of the partes pennarum et dermis of the M. constrictor, is thicker and denser. Beyond the caudal border of the M. constrictor, the M. apterialis scapularis, which is the caudal extension of the M. apterialis cervicalis lateralis, is so thick and dense that it has the appearance of a skeletal muscle (see Figures 7, 11 and 13). It appears, thus, that the total number of muscle fiber bundles exerting a dorsal pull on the ventral cervical feather tract is proportional to the thickness of the subepidermal fat pad of the feather tract and the size of the feather follicles it carries. Furthermore, it appears that an increase in muscle mass can be achieved either by increasing the muscle mass of the smooth apterial muscles alone or by combining smooth apterial muscles with striated subcutaneous muscles.

In the second example, the M. apterialis axillaris and the cranial part of the M. apterialis truncalis exert a dorsal pull on the dorsal edge of the pectoral tract except for the section where it is bordered by the axillary feather tract. In this section, however, the partes pennarum et dermis of the M. subcutaneus thoracoalaris insert on large feather follicles and the F. superficialis, which is tightly attached to the cutis of the dorsal periphery of the pectoral feather tract (see Figures 4A, 8, 11, and 13). In essence, the striated muscle fiber bundles of the M. subcutaneus thoracoalaris replaces the lacking apterial muscles in the region of the axillary feather tract where the smooth muscles take the forms of feather muscles.

The combination of smooth and striated muscles for a single function presents an interesting problem for the control of muscle coordination by the central nervous system. The smooth apterial muscles are innervated by the autonomic nervous system, with the sympathetic nervous system being apparently the stimulatory part (Jegorow 1887, 1890; Langley 1902a, b, c, 1904; Morris 1956; Ostmann et al. 1963; Tetzlaff et al. 1965; Peterson and Ringer 1968; Bennett 1974), and the neural control being integrated through the central nervous system (Osborne 1968, and references therein). In contrast, the striated subcutaneous muscles are innervated by spinal nerves (Yasuda 1964, Sinclair 1973, Bubien-Waluszewska

1985). This means, that the action of the two different muscle types must be controlled and synchronized by a center in the central nervous system that integrates the autonomic and somatic nervous systems.

4.2. Cutaneous and subcutaneous fat tissue

The present observations on the fat tissue and deposits of the turkey complete and clarify the incomplete and very confusing previous information. The present study is also the first one to recognize that fat bodies (Corpora adiposa) are not just energy storage organs, but are strategically located within distinct layers in order to fulfill biomechanical functions.

The fat tissue is stored in three different ways: It is stored as dermal fat in the Stratum profundum of the dermis; it is interlarded in the Fascia superficialis; and it is contained in distinct fat bodies. The fat tissue may regress or increase depending on the metabolic condition of the bird, but a certain amount of fat will always be maintained to satisfy biomechanical functions. Clara (1923), in a detailed histological study, found that plurivacuolar fat cells, which contain many small droplets of fat, consistently occur in large amounts in the Stratum profundum around feather follicles where the fat tissue is subjected to pressure and tension during feather movements. Univacuolar fat cells, which contain a single droplet of fat, occur consistently in the deeper subcutaneous fat bodies.

The present observations on the domestic turkey also clarify the previous confusion regarding the presence or lack of fat deposits underlying the incubation patch (see Barkow 1829; Freund 1926; Lange 1927, 1928). In the region of the incubation patch, there is only a minimal amount of fat in the Stratum profundum of the dermis, but there is a fat body, the Corpus adiposum carinae, in the constrictor layer. This fat body, however, serves as a hydraulic cushion between the keel of the sternum and the overlying skin and subcutaneous layers. It lies under the cutis and is separated from it by the F. superficialis. Therefore, it does not interfere with the increased vascularization of the dermis in the area of the incubation patch, which occurs during incubation for the transfer of heat to the eggs.

Finally, the present study also clarifies the structure of the subepidermal fat pads which typically underlie feather tracts that are characterized by large feathers and a high density of feathers. A subepidermal fat pad is the result of the combination of a large amount of dermal fat in the Stratum profundum of the dermis and a thick, highly interlarded F. superficialis.

### 4.3. Feather movement

The present study also permits an attempt at formulating a hypothesis about the feather raising mechanism. Although several anatomists have tried their hands at finding a functional explanation for the mechanism of feather movement (Seuffert 1862; Langley 1902a, b, c, 1904; Morris 1956; Lucas and Stettenheim 1972), their theories were not satisfying. As Lucas and Stettenheim (1972) admitted, a convincing model would need to specify the fulcrum around which the feather follicle rotates, but no fulcrum was apparent within the avian skin.

However, as the present study shows, each feather follicle is surrounded by dermal fat, and the base of each feather follicle rests on the Fascia superficialis which is interlarded with fat. Fat tissue, in general, acts as a hydrostatic skeleton (Wasserman 1926). This biomechanical function of the dermal and fascial fat had not been realized previously. But if it is taken into account, a new model for the mechanism of the feather movement emerges (see Figure 14).

When the erector feather muscles contract, the feather follicles are rotated into a more vertical position and their bases are pushed into the underlying Fascia superficialis. This compresses the fascia, thereby increasing its internal pressure. By becoming turgid, the fascia serves as a hydraulic skeleton to stabilize the raised feathers.

4.4. Testing and outlook

As mentioned earlier, the cutaneous and subcutaneous structures in birds, and vertebrates in general, have usually been studied in isolated pieces, often quite dissociated from their horizontal or vertical neighbors. Although the present study was able to build on the results of previous studies, the present study shows the benefit of and need for studying the skin as a complex biomechanical system whose components interact in multiple ways. It is an additional step towards taking a holistic look at the integument and its biomechanical, physiological and structural properties.

The findings and the hypotheses regarding constructional principles and functional explanations of this study can be tested through future comparisons with other individuals, species and genera. The testing of the validity of the functional interpretations can be done by using electromyography to measure the degree of synchronization between smooth and dermal muscles, by pressure measurements of the fat bodies, by strain measurements (with gauges) of the fascial layers, and by using neurophysiological methods to trace the neural circuits innervating the smooth and striated muscles.

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# APPENDIX

Table 1. Size of contour feathers, bristles, and semibristles from the head and neck of Meleagris gallopavo (specimen DGH1♀).

| Feather Type | Skin Type | Pteryla | Site of Sampling | N | Mean long diameter (mm) of rachis and standard error | Range (mm) | Mean length (mm) of rachis and standard error | Range (mm) |
|---|---|---|---|---|---|---|---|---|
| Semibristles | Wrinkled | ophthalmica | on eyelids and dorsal to eye | 24 | 0.18 ± 0.01 | 0.12 - 0.27 | 1.21 ± 0.06 | 0.69 - 1.86 |
| | Wrinkled | ophthalmica | around nasal operculum | 6 | 0.36 ± 0.04 | 0.24 - 0.54 | 1.80 ± 0.13 | 1.73 - 2.16 |
| | Wrinkled | ophthalmica | over Arc. jugalis | 6 | 0.25 ± 0.02 | 0.18 - 0.30 | 3.19 ± 0.31 | 2.52 - 4.50 |
| Bristles | Wrinkled | gularis | dorsal and cranial to eye | 5 | 0.29 ± 0.01 | 0.24 - 0.30 | 2.84 ± 0.38 | 1.26 - 3.60 |
| | Wrinkled | gularis | dorsal to eye | 9 | 0.31 ± 0.01 | 0.30 - 0.36 | 4.82 ± 0.60 | 2.58 - 7.90 |
| | Wrinkled | gularis | caudal and ventral to ear | 16 | 0.40 ± 0.02 | 0.30 - 0.45 | 11.07 ± 0.63 | 5.96 - 13.70 |
| Contour feathers | Wrinkled | auricularis | around external ear opening | 9 | 0.35 ± 0.03 | 0.18 - 0.42 | not available | not available |
| | Carunculate | occipitalis | dorsal to eye | 14 | 0.19 ± 0.01 | 0.12 - 0.24 | 2.60 ± 0.26 | 1.90 - 4.50 |
| | Carunculate | occipitalis | dorsal to cervical caruncles | 9 | 0.49 ± 0.02 | 0.45 - 0.60 | 6.71 ± 0.35 | 5.51 - 8.64 |
| | Smooth | cervicalis ventralis | immediately caudal to cervical caruncles | 30 | 0.61 ± 0.04 | 0.25 - 0.95 | not available | not available |
| | Smooth | cervicalis ventralis | on subepidermal fat pad | 25 | 1.60 ± 0.02 | 1.48 - 1.75 | not available | not available |

Table 2. Long diameter of the rachis base of contour feathers (1 unit = 0.025mm) in the ventral cervical feather tract of Meleagris gallopavo (DGH1♀). A8-A29 and B4-B28 refer to the grid lines lying cranial to each feather (see Fig. 4). The thick line across the table indicates the border of the subepidermal fat pad.

| A \ B | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 8 | 16 | | 23 | 22 | | 32 | 36 | | 30 | | | | | | | | | | | | | | | | |
| 9 | | 5 | 16 | 30 | | | | | | | | | | | | | | | | | | | | | |
| 10 | | | | 24 | 28 | | 28 | 31 | 35 | | | | | | | | | | | | | | | | |
| 11 | 3 | 3 | 4 | | 23 | | 32 | 32 | 29 | 29 | | | | | | | | | | | | | | | |
| 12 | | 4 | 5 | 15 | 28 | | 31 | | 36 | 40 | 41 | 41 | 40 | 38 | | | | | | | | | | | |
| 13 | | | 4 | 5 | 12 | | 20 | | 27 | 40 | 40 | 50 | 52 | 50 | 38 | | | | | | | | | | |
| 14 | | | | | | | | | | | | | | | 37 | | | | | | | | | | |
| 15 | | | | | 21 | | 30 | | 30 | 40 | 42 | 40 | 40 | 45 | 45 | 42 | | | | | | | | | |
| 16 | | | | | | | | | | | 31 | 43 | 40 | 50 | 55 | 55 | 50 | | | | | | | | |
| 17 | | | | | | | 10 | 10 | 16 | | 30 | 50 | 50 | 55 | 55 | 50 | 55 | 55 | | | | | | | |
| 18 | | | | | | | | | | 11 | | 13 | 35 | 48 | 50 | 57 | 61 | 60 | 60 | | | | | | |
| 19 | | | | | | | | | | | 15 | 20 | 33 | 50 | 52 | 58 | 60 | 60 | 60 | 53 | 46 | | | | |
| 20 | | | | | | | | | | | | | 10 | 38 | 49 | 48 | 55 | | 57 | 56 | 55 | 60 | 60 | 57 | |
| 21 | | | | | | | | | | | | | | | | | | | | | | | | 53 | 20 |
| 22 | | | | | | | | | | | | | | | | | | | | | | | | 60 | 45 |
| 23 | | | | | | | | | | | | | | | | | | | | | | | 68 | 65 | 60 |
| 24 | | | | | | | | | | | | | | | | | | | | 59 | 60 | | 70 | 68 | 59 |
| 25 | | | | | | | | | | | | | | | 25 | 46 | 58 | | 57 | 48 | 55 | 60 | 60 | 70 | 68 |
| 26 | | | | | | | | | | | | | | | | | 38 | | 50 | 56 | 55 | 57 | 60 | 62 | 70 |
| 27 | | | | | | | | | | | | | | | | 20 | 56 | | 60 | 65 | 65 | 61 | 65 | 60 | 60 |
| 28 | | | | | | | | | | | | | | | | | 10 | | 50 | 51 | 65 | 60 | 68 | 60 | 60 |
| 29 | | | | | | | | | | | | | | | | | 20 | | 61 | 65 | 54 | 60 | 70 | 70 | NA |

Table 3. Short diameter of the rachis base of contour feathers (1 unit = 0.025mm) in the ventral cervical feather tract of Meleagris gallopavo (DGH1♀). A8-A29 and B4-B28 refer to the grid lines lying cranial to each feather (see Fig. 4). The thick line across the table indicates the border of the subepidermal fat pad.

| A \ B | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 8 | 7 | | 21 | 20 | | 25 | 29 | | 25 | | | | | | | | | | | | | | | | |
| 9 | | 3 | 10 | 28 | | | | | | | | | | | | | | | | | | | | | |
| 10 | | | | 18 | 23 | | 23 | 27 | 28 | | | | | | | | | | | | | | | | |
| 11 | 2 | 2 | 3 | | 22 | | 31 | 31 | 28 | 29 | | | | | | | | | | | | | | | |
| 12 | | 3 | 4 | 12 | 13 | | 28 | | 28 | 32 | 35 | 37 | 35 | 32 | | | | | | | | | | | |
| 13 | | | 3 | 4 | 7 | | 16 | | 27 | 32 | 32 | 37 | 40 | 41 | 38 | | | | | | | | | | |
| 14 | | | | | | | | | | | | | | | 37 | | | | | | | | | | |
| 15 | | | | | 15 | | 25 | | 25 | 35 | 35 | 40 | 40 | 40 | 40 | 41 | | | | | | | | | |
| 16 | | | | | | | 15 | | | | 30 | 30 | 37 | 45 | 50 | 50 | 50 | | | | | | | | |
| 17 | | | | | | | 7 | 8 | 8 | | 26 | 42 | 40 | 50 | 45 | 51 | 44 | 43 | | | | | | | |
| 18 | | | | | | | | | | 6 | | 10 | 31 | 36 | 40 | 46 | 49 | 53 | 50 | | | | | | |
| 19 | | | | | | | | | | | 5 | 10 | 30 | 44 | 45 | 50 | 57 | 57 | 55 | 52 | 46 | | | | |
| 20 | | | | | | | | | | | | | 10 | 31 | 42 | 42 | 50 | | 56 | 55 | 55 | 54 | 60 | 56 | |
| 21 | | | | | | | | | | | | | | | | | | | | | | | | 45 | 15 |
| 22 | | | | | | | | | | | | | | | | | | | | | | | | 50 | 40 |
| 23 | | | | | | | | | | | | | | | | | | | | | | | 55 | 50 | 50 |
| 24 | | | | | | | | | | | | | | | | | | | | 59 | 55 | | 60 | 62 | 58 |
| 25 | | | | | | | | | | | | | | | 10 | 45 | 52 | | 55 | 40 | 44 | 50 | 58 | 57 | 60 |
| 26 | | | | | | | | | | | | | | | | 34 | 44 | | 50 | 48 | 50 | 44 | 55 | NA | 64 |
| 27 | | | | | | | | | | | | | | | | 20 | 52 | | 52 | 55 | 65 | 60 | 60 | 58 | 55 |
| 28 | | | | | | | | | | | | | | | | | 6 | | 38 | 45 | 60 | 60 | 60 | 60 | 50 |
| 29 | | | | | | | | | | | | | | | | | 15 | | 55 | 60 | 50 | 50 | NA | 60 | 60 |

Table 4: Characteristics of the apterial muscles of the neck and thorax of <u>Meleagris gallopavo</u> (DGH1♀).

| Apterial muscles | Thickness of fiber bundles | Density of fiber bundles per 10mm | N | Average length of tendinous segment ± std. error | Range (mm) | Average length of muscular segment ± std. error | Range (mm) |
|---|---|---|---|---|---|---|---|
| M. apt. cervicalis lat., cran. part | thin | 2 | 4 | 1.46 ± 0.02 | 1.17 - 1.75 | 1.75 ± 0.15 | 1.46 - 2.19 |
| M. apt. cervicalis lat., caud. part | intermed. | 8 | 8 | 0.66 ± 0.04 | 0.58 - 0.73 | 1.27 ± 0.12 | 1.16 - 1.75 |
| M. apt. cervicalis ventralis | thick | 14 | 8 | 0.58 ± 0.06 | 0.44 - 0.88 | 0.80 ± 0.14 | 0.44 - 1.46 |
| M. apt. scapularis, cran. part | thick | 12 | 8 | 0.66 ± 0.03 | 0.58 - 0.73 | 1.27 ± 0.25 | 0.29 - 2.04 |
| M. apt. scapularis, caud. part | thin | 4 | 8 | 0.68 ± 0.03 | 0.58 - 0.73 | 1.25 ± 0.21 | 0.30 - 2.04 |
| M. apt. axillaris | thin | 3 | 4 | 1.39 ± 0.07 | 1.17 - 1.46 | 1.17 ± 0.21 | 0.88 - 1.75 |
| M. apt. truncalis, cran. part | thin | 4 | 2 | 5.11 ± 0.73 | 4.38 - 5.84 | 0.37 ± 0.07 | 0.29 - 0.44 |
| M. apt. truncalis, caud. part | thick | 15 | 6 | 0.81 ± 0.17 | 0.44 - 1.46 | 3.07 ± 0.62 | 2.68 - 5.84 |
| M. apt. pectoralis | intermed. | 13 | 11 | 0.69 ± 0.02 | 0.58 - 0.73 | 5.49 ± 0.44 | 2.92 - 8.47 |
| M. apt. sternalis | thin | 7 | 7 | 1.69 ± 0.21 | 1.31 - 2.92 | 2.23 ± 0.32 | 1.46 - 3.65 |

Table 5. Synonymies and homologies of the avian M. constrictor



| Name | Author |
|---|---|
| M. constrictor colli cervicalis | Homberger and Meyers (1989; see references therein for additional synonymies) |
| M. constrictor colli | Owen 1842; Fisher and Goodman 1955; Goodman and Fisher 1962 |
| M. constrictor colli and M. dermotemporalis | Helm 1886 |
| M. sphincter colli | Fürbringer 1888; Beddard 1890 |
| M. dermotemporalis | Burt 1930 |

Table 6. Summary of the layers supporting the feather tracts and apteria in the head, neck, and thorax of Meleagris gallopavo.

| | Pt. auricularis | Pt. ophthalmica | Pt. gularis | Pt. occipitalis | Pt. cervicalis dorsalis |
|---|---|---|---|---|---|
| Texture of skin | wrinkled | wrinkled | wrinkled | carunculate | smooth |
| Thickness of dermal fat | intermediate | very thin | very thin | very thin | thin-intermediate-thick |
| Mm.pennarum | present | present | present | present | present |
| Thickness of Mm.apteriales | - | - | - | - | - |
| Density of Mm.apteriales | - | - | - | - | - |
| Connection cutis-F.supf | fused | tight-fused | tight-fused | tight-fused | tight and fused |
| Thickness of F.supf | intermediate | intermediate | intermediate-thin | intermediate-thin | intermediate-thick |
| Fat bodies of F.supf | - | C.fac | C.fac | - | - |
| Connection F.supf-Str.constrictor | fused | fused | fused | loose-tight | tight-fused |
| Fat bodies of Str.constrictor | - | - | - | - | - |
| Subcutaneous muscles | - | - | M.c | M.c | M.c |

(cont'd)

| | Pt. cervicalis ventralis | Pt. interscapularis | Pt. dorsalis | Pt. scapularis | Pt. pectoralis | Pt. axillaris |
|---|---|---|---|---|---|---|
| Texture of skin | smooth | smooth | smooth | smooth | smooth | smooth |
| Thickness of dermal fat | thin-intermediate-thick | thick | thick | thick | thick | thick |
| Mm.pennarum | present | present | present | present | present | present |
| Thickness of Mm.apteriales | - | - | - | - | - | - |
| Density of Mm.apteriales | - | - | - | - | - | - |
| Connection cutis-F.supf | fused | fused | fused | fused | tight | tight |
| Thickness of F.supf | thin-thick | thick | thick | thick | thick | thick |
| Fat bodies of F.supf | - | - | C.ral | C.csca<br>C.spal | - | C.sbal |
| Connection F.supf-Str.constrictor | loose-tight-fused | fused | tight | tight | tight-loose | tight |
| Fat bodies of Str.constrictor | C.singl | - | - | - | C.thor | - |
| Subcutaneous muscles | M.c | M.sb.dor | M.sb.dor<br>M.sb.doral<br>M.sb.abdal | M.sb.doral<br>M.sb.abdal | M.sb.thoral<br>M.sb.thoabd | M.sb.thoral |

(cont'd)

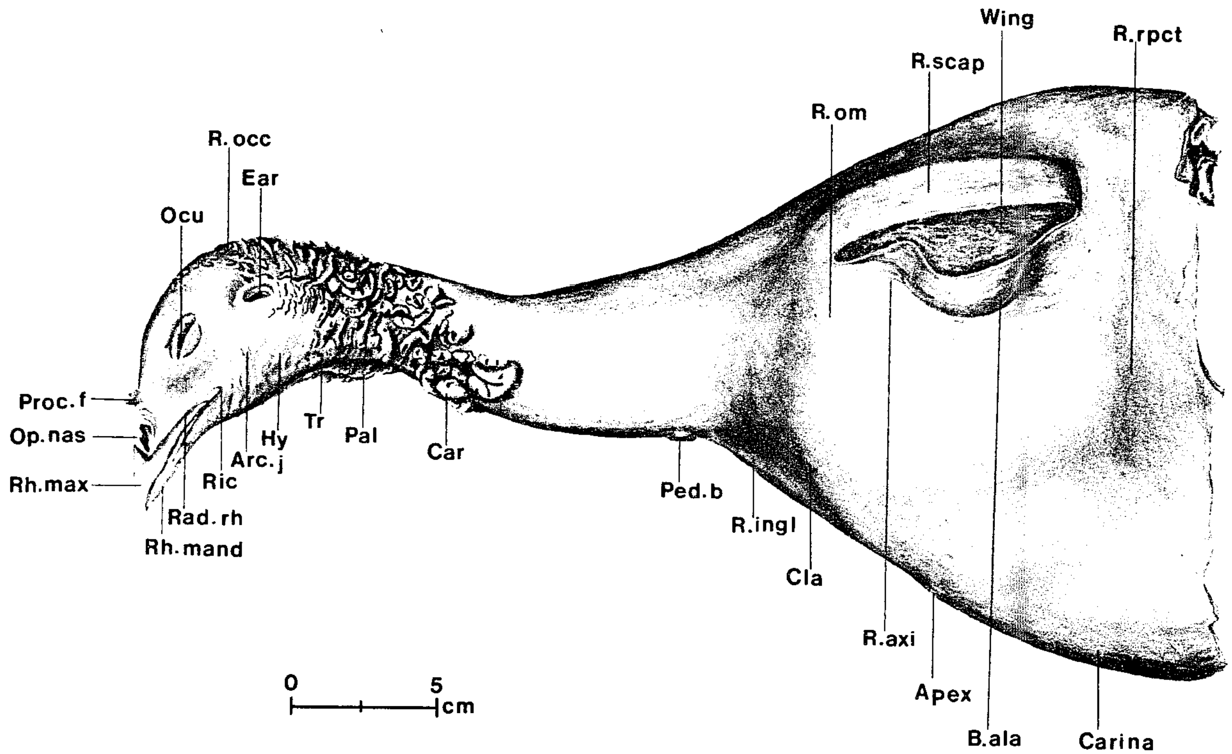
| | Pt. sternalis | Apt. cervicale laterale | Apt. cervicale ventrale | Apt. scapulare | Apt. spinale |
|---|---|---|---|---|---|
| Texture of skin | smooth | smooth | smooth | smooth | smooth |
| Thickness of dermal fat | intermediate | thin-intermediate-thick | thin | thick-thin | intermediate |
| Mm.pennarum | present | - | - | - | - |
| Thickness of Mm.apteriales | - | thin-intermediate | thick | thick-intermediate-thin | intermediate |
| Density of Mm.apteriales | - | low-medium | high | high-medium-low | low |
| Connection cutis-F.supf | tight | fused-tight-loose | fused | loose-tight | tight |
| Thickness of F.supf | thick | thin-thick | thin | thick | intermediate |
| Fat bodies of F.supf | - | C.csca | - | C.csca C.spal | - |
| Connection F.supf-Str.constrictor | loose | loose-tight | tight | loose-tight | tight |
| Fat bodies of Str.constrictor | - | - | C.singl | - | - |
| Subcutaneous muscles | - | M.c | M.c | M.sb.dor | - |

(cont'd)

| | Apt. pectorale | Apt. sternale | Apt. axillare | Apt. truncale |
|---|---|---|---|---|
| Texture of skin | smooth | smooth | smooth | smooth |
| Thickness of dermal fat | intermediate-thick | thin-very thin | thin-intermediate-thick | thick |
| Mm.pennarum | - | - | - | - |
| Thickness of Mm.apteriales | intermediate | thin | thin | thin-intermediate-thick |
| Density of Mm.apteriales | high | medium | low | low-medium-high |
| Connection cutis-F.supf | loose | tight | fused | loose |
| Thickness of F.supf | thick | thick | thin | thick |
| Fat bodies of F.supf | - | - | C.sbal | C.sbal |
| Connection F.supf-Str.constrictor | loose | loose | tight-fused | tight |
| Fat bodies of Str.constrictor | - | C.car | C.axi | - |
| Subcutaneous muscles | M.sb.thoabd | - | - | M.sb.abdal<br>M.sb.thoral<br>M.sb.thoabd |

Figure legends and figures

Figure 1. Topography and palpable structures of the right side of the head, neck and thorax in Meleagris gallopavo (specimen DGH1♀). The original drawing representing the right side was inverted, and all feathers have been omitted from the drawing. Abbreviations: Apex palpable Apex carinae; Arc.j palpable jugal bar; B.ala base of the wing; Car cervical caruncles; Carina palpable keel of sternum; Cla palpable clavicle; Ear external ear opening; Hy palpable hyoid horn; Ocu eye; Op.nas nasal operculum; Pal dewlap; Ped.b peduncle of beard; Proc.f frontal process; R.axi axillary region; R.ingl region over the crop; R.occ occipital region; R.om region over the shoulder joint; R.rpct region caudal to the pectoral muscle; R.sca shoulder region; Rad.rh root of the rhamphotheca; Rh.mand mandibular rhamphotheca; Rh.max maxillary rhamphotheca; Ric corner of the mouth or rictus; Tr palpable trachea; Wing cross-section through base of wing.



Wing
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R.scap
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R.axi
Apex
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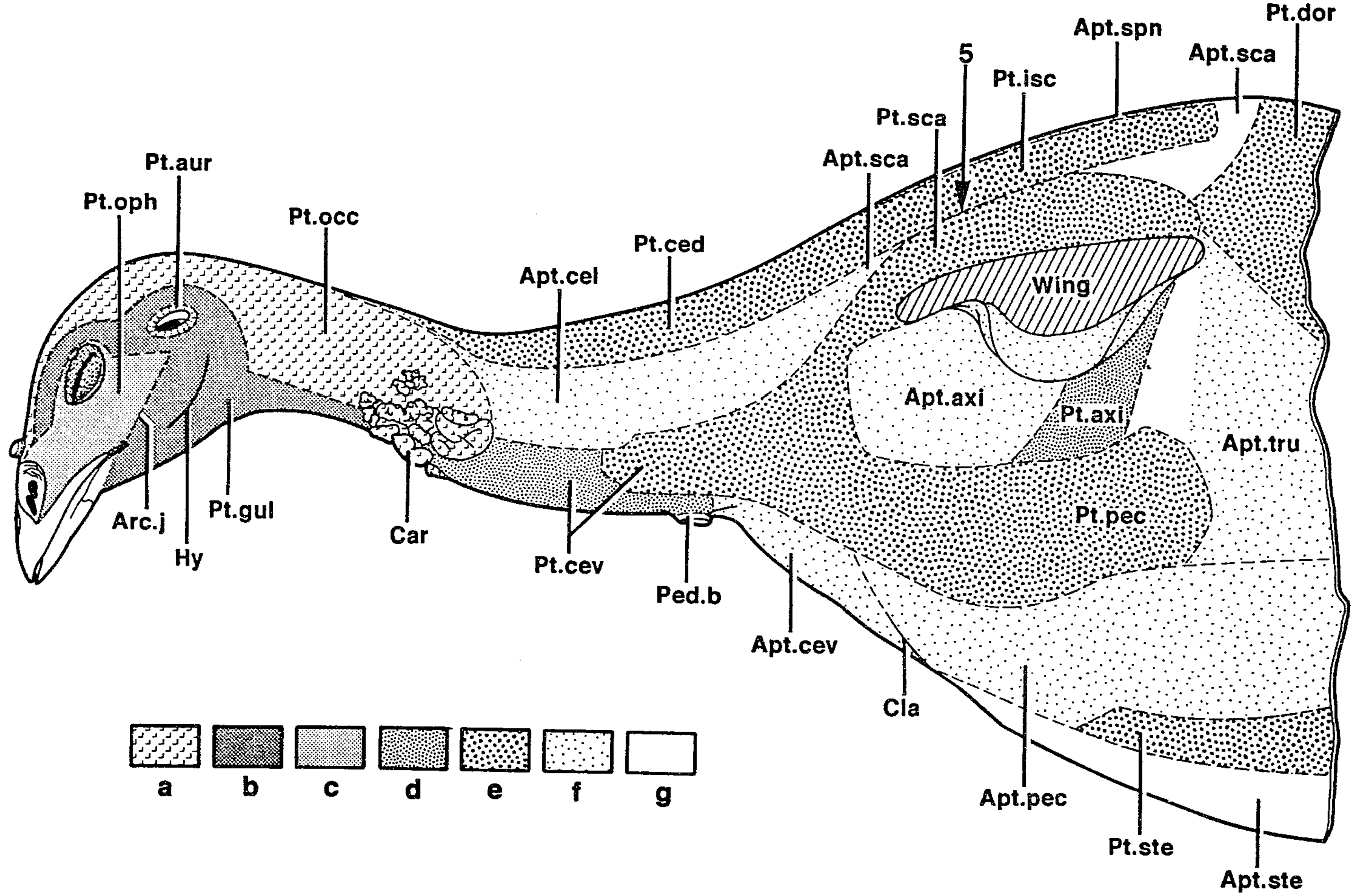
cm


Figure 1

Figure 2. Diagram of a lateral view of the distribution pattern of the different skin and feather types on the head, neck and thorax in Meleagris gallopavo. The borders between major pterylae and apteria are indicated by dashed lines. Symbols: a carunculate skin with small contour feathers; b-c wrinkled skin (b with bristles, c with semibristles); d-g smooth skin (d with small contour feathers, e with large contour feathers, f with semiplumes, g bare). The wrinkled skin of the auricular feather tract around the external ear opening bears small contour feathers, and that of the eye lids bears down feathers in addition to the semibristles. The numeral 5 indicates the level of the borderline between the cranial part of the scapular apterium bearing semiplumes and the bare caudal part. Abbreviations: Apt.axi Apterium axillare; Apt.cel Apterium cervicale laterale; Apt.cev Apterium cervicale ventrale; Apt.pec Apterium pectorale; Apt.sca Apterium scapulare; Apt.spn Apterium spinale; Apt.ste Apterium sternale; Apt.tru Apterium truncale; Arc.j palpable jugal arch; Car cervical caruncles; Cla palpable clavicle; Hy palpable hyoid horn; Ped.b peduncle of beard; Pt.aur Pteryla auricularis; Pt.axi Pteryla axillaris; Pt.ced Pteryla cervicalis dorsalis; Pt.cev Pteryla cervicalis ventralis; Pt.dor Pteryla dorsalis; Pt.gul Pteryla gularis; Pt.isc Pteryla interscapularis; Pt.occ Pteryla occipitalis; Pt.oph Pteryla ophthalmica; Pt.pec Pteryla pectoralis; Pt. sca Pteryla scapularis; Pt.ste Pteryla sternalis; Wing cross-section through base of wing.



Pt.dor
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Apt.sca
5
Pt.isc
Pt.sca
Apt.sca
Pt.aur
Pt.oph
Pt.occ
Pt.ced
Apt.cel
Wing
Apt.axi
Pt.axi
Apt.tru
Pt.pec
Arc.j
Pt.gul
Hy
Car
Pt.cev
Ped.b
Apt.cev
Cla
Apt.pec
Pt.ste
Apt.ste
a
b
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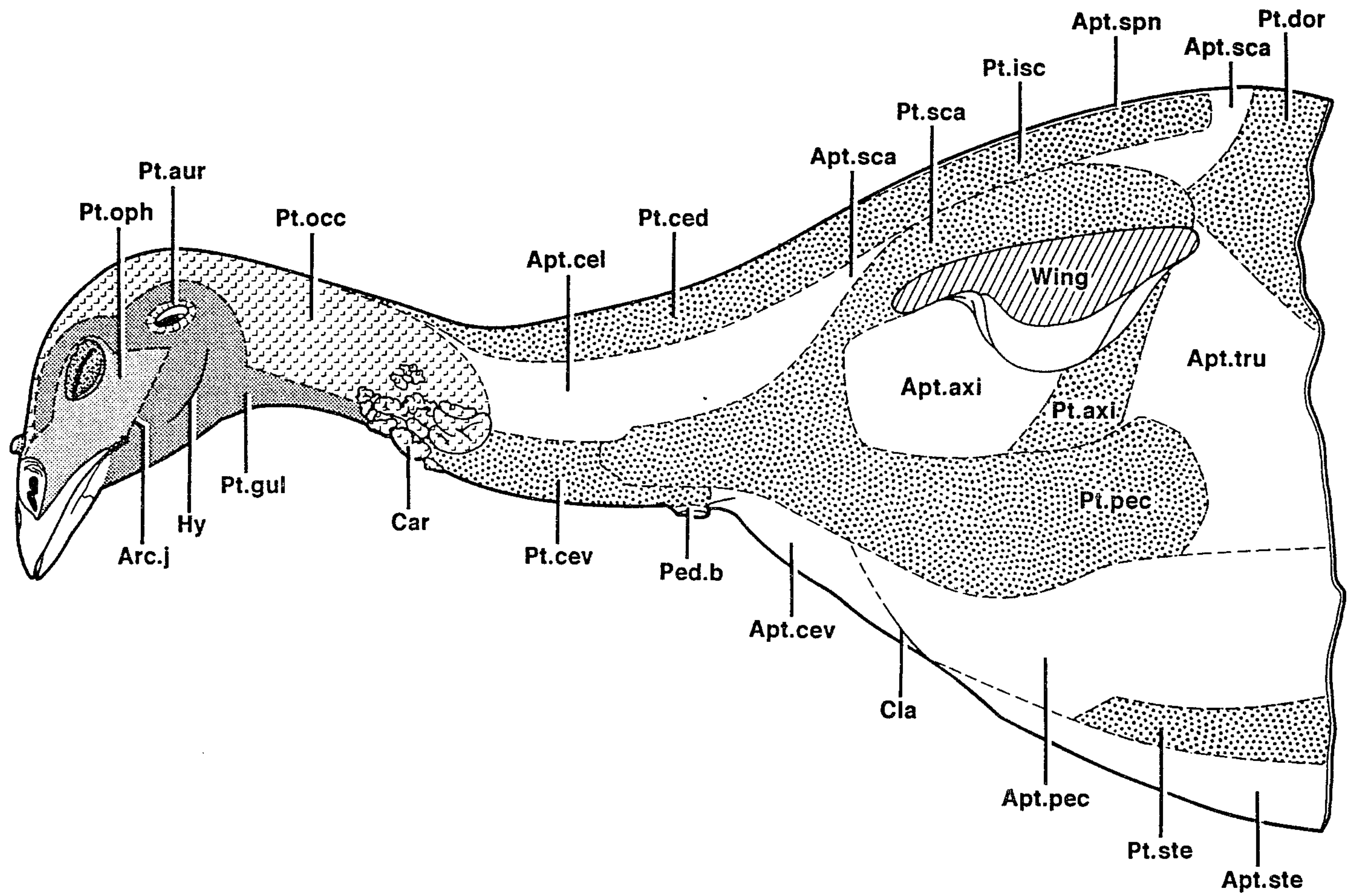
Figure 2

Figure 3. Diagram of a lateral view of the pterylography of the head, neck and thorax in Meleagris gallopavo. The borders between major pterylae and apteria are indicated by dashed lines. Abbreviations: Apt.axi Apterium axillare; Apt.cel Apterium cervicale laterale; Apt.cev Apterium cervicale ventrale; Apt.pec Apterium pectorale; Apt.sca Apterium scapulare; Apt.spn Apterium spinale; Apt.ste Apterium sternale; Apt.tru Apterium truncale; Arc.j palpable jugal arch; Car cervical caruncles; Cla palpable clavicle; Hy palpable hyoid horn; Ped.b peduncle of beard; Pt.aur Pteryla auricularis; Pt.axi Pteryla axillaris; Pt.ced Pteryla cervicalis dorsalis; Pt.cev Pteryla cervicalis ventralis; Pt.dor Pteryla dorsalis; Pt.gul Pteryla gularis; Pt.isc Pteryla interscapularis; Pt.occ Pteryla occipitalis; Pt.oph Pteryla ophthalmica; Pt.pec Pteryla pectoralis; Pt. sca Pteryla scapularis; Pt.ste Pteryla sternalis; Wing cross-section through base of wing.


Apt.spn
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Pt.aur
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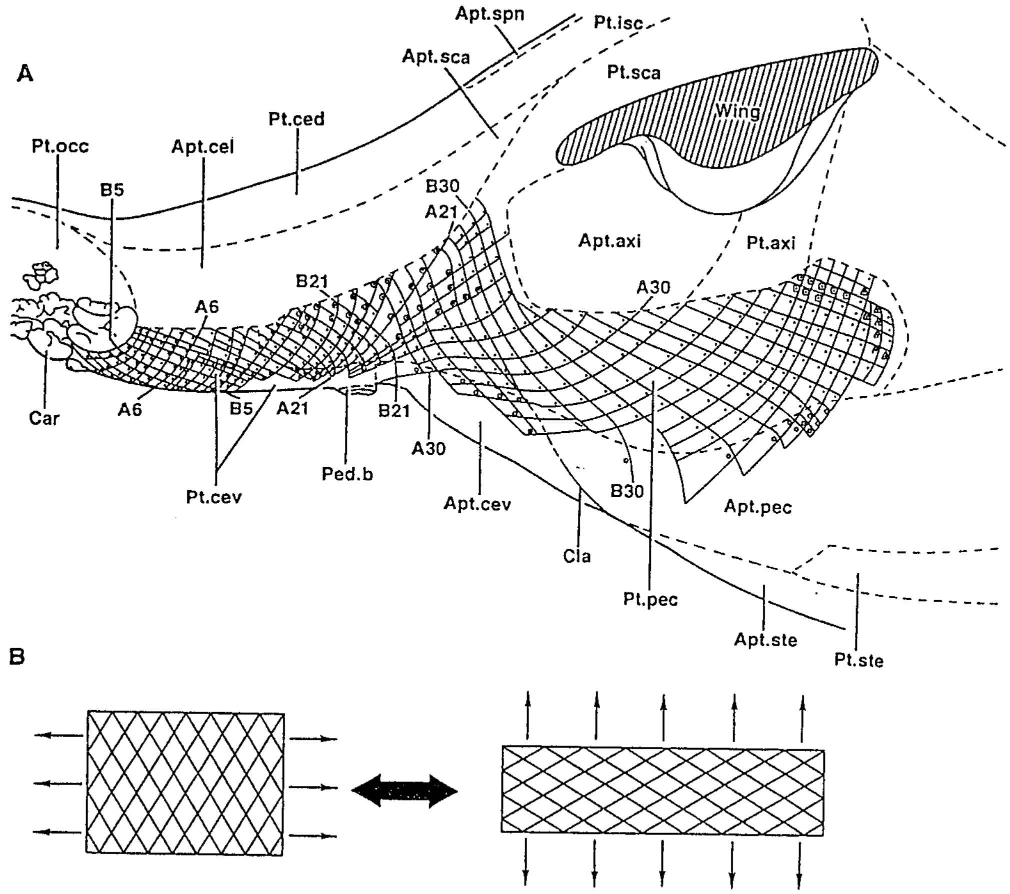
Pt.ced
Apt.cel
Wing
Apt.tru
Apt.axi
Pt.axi
Pt.pec
Pt.gul
Hy
Arc.j
Car
Pt.cev
Ped.b
Apt.cev
Cla
Apt.pec
Pt.ste
Apt.ste

Figure 3

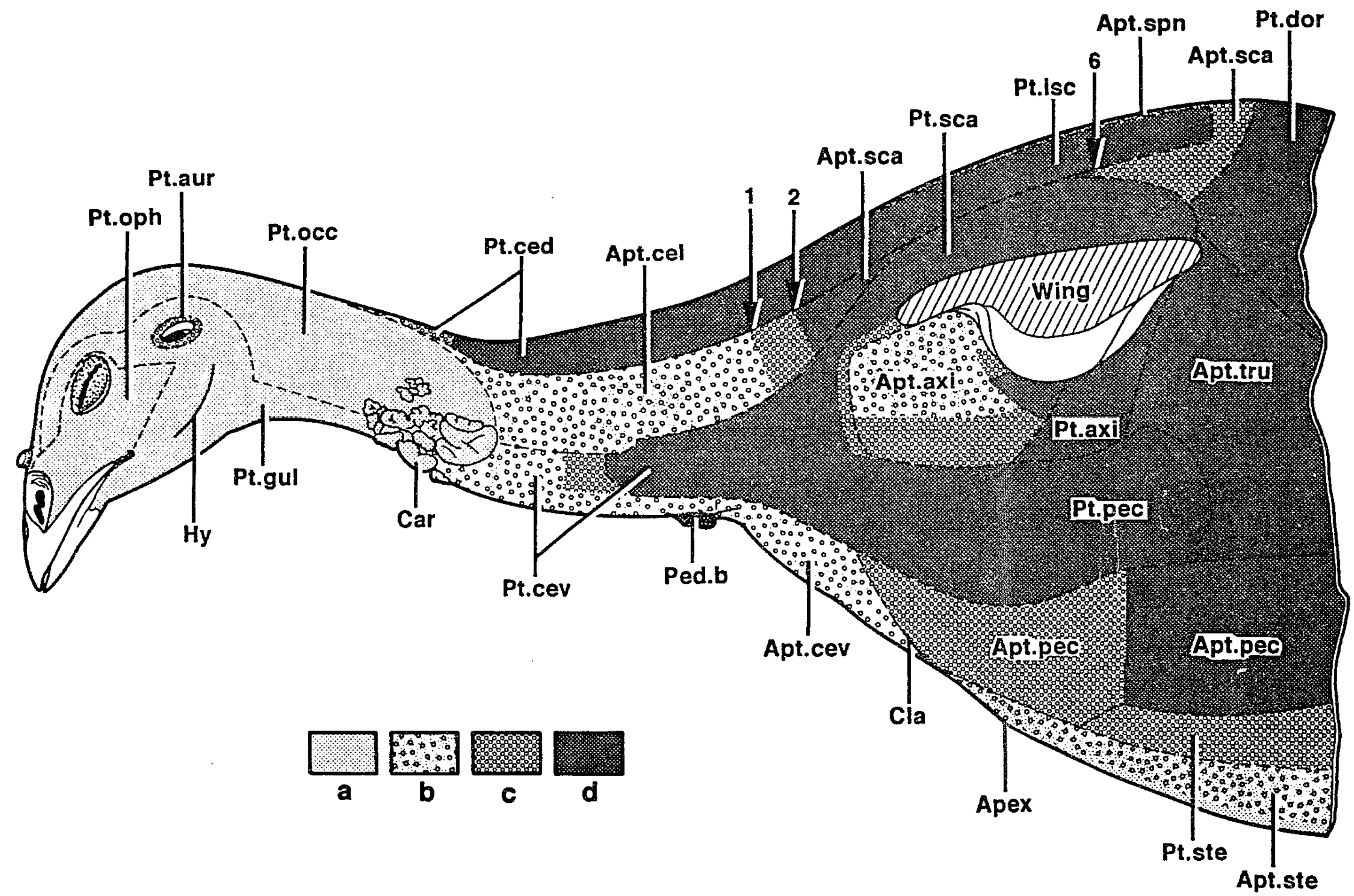
Figure 4. A. Diagram of a lateral view of the feather arrangement in the ventral cervical and pectoral feather tracts and the attachments to individual feather follicles by striated subcutaneous muscles in Meleagris gallopavo. The borders between major pterylae and apteria are indicated by dashed lines. The grid of diagonally crossing lines highlights the orientation of the feather rows and allows the identification of individual feather follicles. A6-A30 represent samples of the numbered grid lines running from cranioventral to caudodorsal; B5-B30 represent samples of the numbered grid lines running from craniodorsal to caudoventral. The very small feather follicles on the caudoventral portion of the ventral cervical feather tract are not recorded. B. Diagram showing how diagonal grid of parallelograms can be deformed by longitudinal and transversal forces while the lengths of the grid lines do not change. Symbols: solid dots represent follicles of contour feather; Solid dots in circles represent feather follicles to which M. constrictor pars pennarum attaches; solid dots in squares represent feather follicles to which M. subcutaneous thoracoalaris pars pennarum attaches; solid dots in triangles represent feather follicles to which M. subcutaneous thoracoabdominalis pars pennarum attaches; small circles represent follicles of semiplumes in apteria. Abbreviations: Apt.axi Apterium axillare; Apt.cel Apterium cervicale laterale; Apt.cev Apterium cervicale ventrale; Apt.pec Apterium pectorale; Apt.sca Apterium scapulare; Apt.spn Apterium spinale; Apt.ste Apterium sternale; Car cervical caruncles; Cla palpable clavicle; Ped.b peduncle of beard; Pt.axi Pteryla axillaris; Pt.ced Pteryla cervicalis dorsalis; Pt.cev Pteryla cervicalis ventralis; Pt.occ Pteryla occipitalis; Pt.pec Pteryla pectoralis; Pt. sca Pteryla scapularis; Pt.ste Pteryla sternalis; Wing cross-section through base of wing.



A
Apt.spn
Pt.isc
Apt.sca
Pt.sca
Wing
Pt.ced
Pt.occ
Apt.cel
B5
B30
A21
Apt.axi
Pt.axi
B21
A6
A30
Car
A6
B5
A21
B21
A30
Ped.b
Pt.cev
Apt.cev
B30
Apt.pec
Cla
Pt.pec
Apt.ste
Pt.ste
B


Figure 4

Figure 5. Diagram of a lateral view of the distribution pattern of different amounts of the dermal fat within the Stratum profundum of the dermis of the head, neck and thorax in Meleagris gallopavo. The borders between major overlying pterylae and apteria are indicated by dashed lines. Symbols: a minimal; b little; c intermediate amount and thickness; d large amount-thick. Numerals: Levels of borderlines that coincide with borderlines identified by the same numbers in other Figures. Abbreviations: Apex palpable; Apex carinae; Apt.axi Apterium axillare; Apt.cel Apterium cervicale laterale; Apt.cev Apterium cervicale ventrale; Apt.pec Apterium pectorale; Apt.sca Apterium scapulare; Apt.spn Apterium spinale; Apt.ste Apterium sternale; Apt.tru Apterium truncale; Car overlying cervical caruncles; Cla palpable clavicle; Ped.b peduncle of beard; Pt.aur Pteryla auricularis; Pt.axi Pteryla axillaris; Pt.ced Pteryla cervicalis dorsalis; Pt.cev Pteryla cervicalis ventralis; Pt.dor Pteryla dorsalis; Pt.gul Pteryla gularis; Pt.isc Pteryla interscapularis; Pt.occ Pteryla occipitalis; Pt.oph Pteryla ophthalmica; Pt.pec Pteryla pectoralis; Pt. sca Pteryla scapularis; Pt.ste Pteryla sternalis; Wing cross-section through base of wing.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Apt.sca
6
Pt.isc
Pt.sca
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Pt.aur
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Apt.cel
1
2
Wing
Apt.axi
Apt.tru
Pt.axi
Pt.pec
Pt.gul
Hy
Car
Pt.cev
Ped.b
Apt.cev
Apt.pec
Apt.pec
Cla
Apex
Pt.ste
Apt.ste
a
b
c
d

Figure 5

Figure 6. Generalized reconstruction of the cutaneous and subcutaneous structures of Meleagris gallopavo. The structures are shown in a section, except for the cutis in the center between the numbered feather follicles, where the dermis and part of the Fascia superficialis were removed to show the feather muscles and the various parts of the Lamina elastica. Abbreviations: Caud caudal; Cran cranial; Epid epidermis; F.supf. Fascia superficialis; Foll epidermal layer of the feather follicle; Lam.elas Lamina elastica; Lam.elas.epim epimysial part of the Lamina elastica; M.apt M. apterialis; M.depr M. depressor; M.erec M. erector; M.sb striated subcutaneous muscle; M.sb.penn fascicle of the pars pennarum of a subcutaneous muscle; Pap.derm pulp cavity of the feather follicle; Penn.cont countour feather; Str.prof Stratum profundum of dermis; Str.supf Stratum superficialis of dermis. 1-3 identify specific feather follicles.

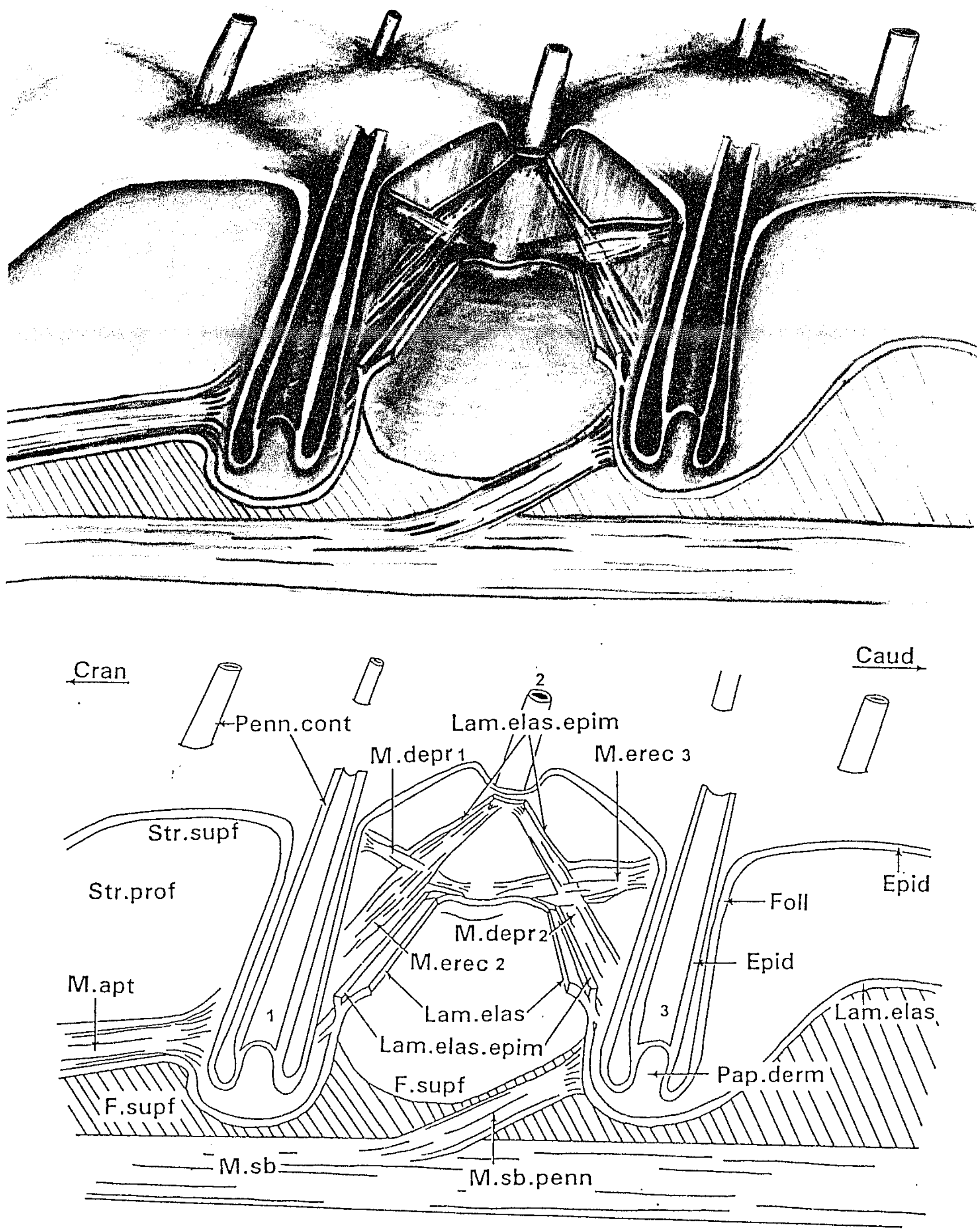
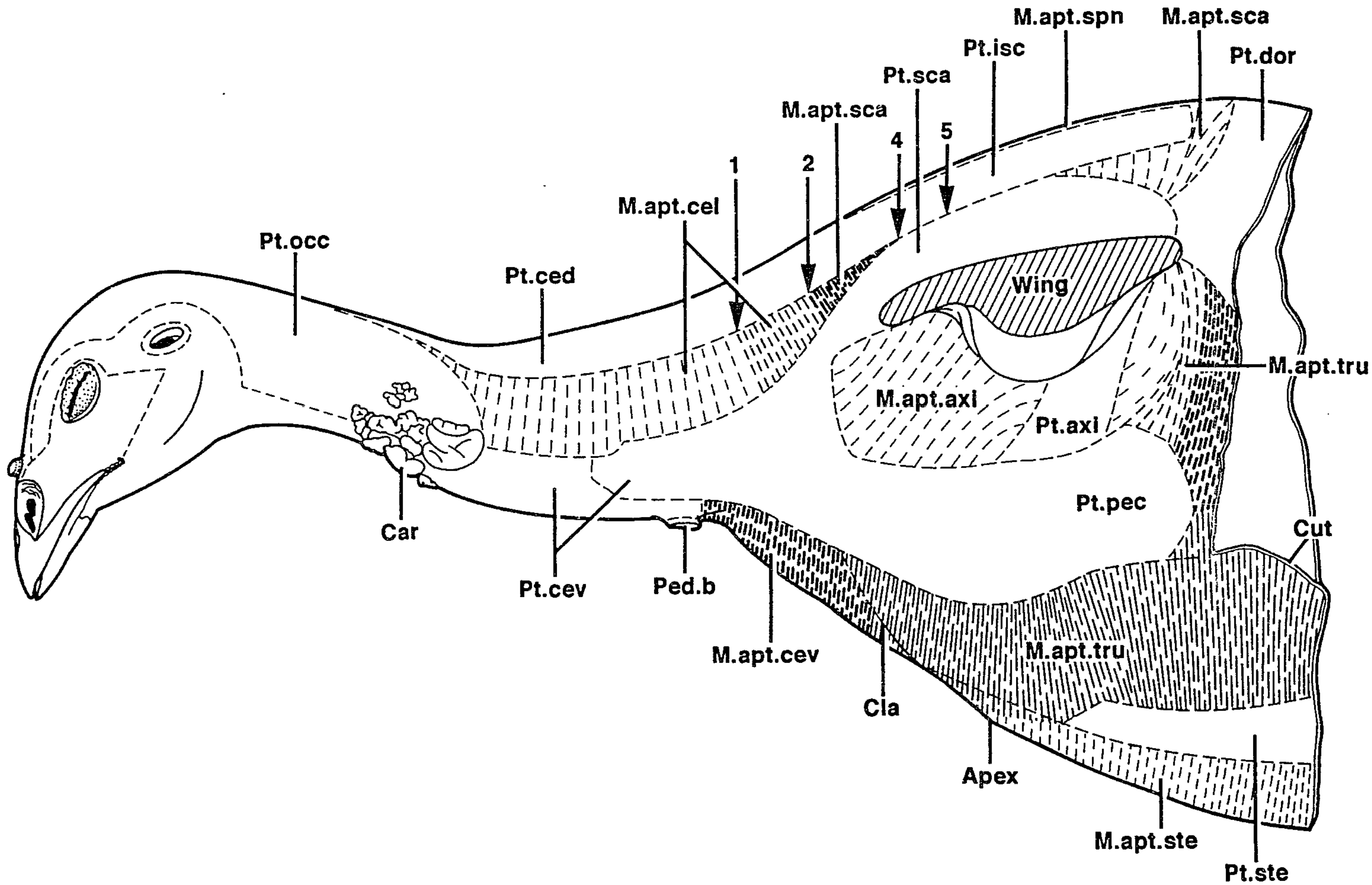

Cran
Caud
2
Penn.cont
Lam.elas.epim
M.depr1
M.erec 3
Str.supf
Str.prof
Foll
Epid
M.depr2
M.erec 2
Epid
M.apt
1
3
Lam.elas
Lam.elas
Lam.elas.epim
Pap.derm
F.supf
F.supf
M.sb
M.sb.penn

Figure 6

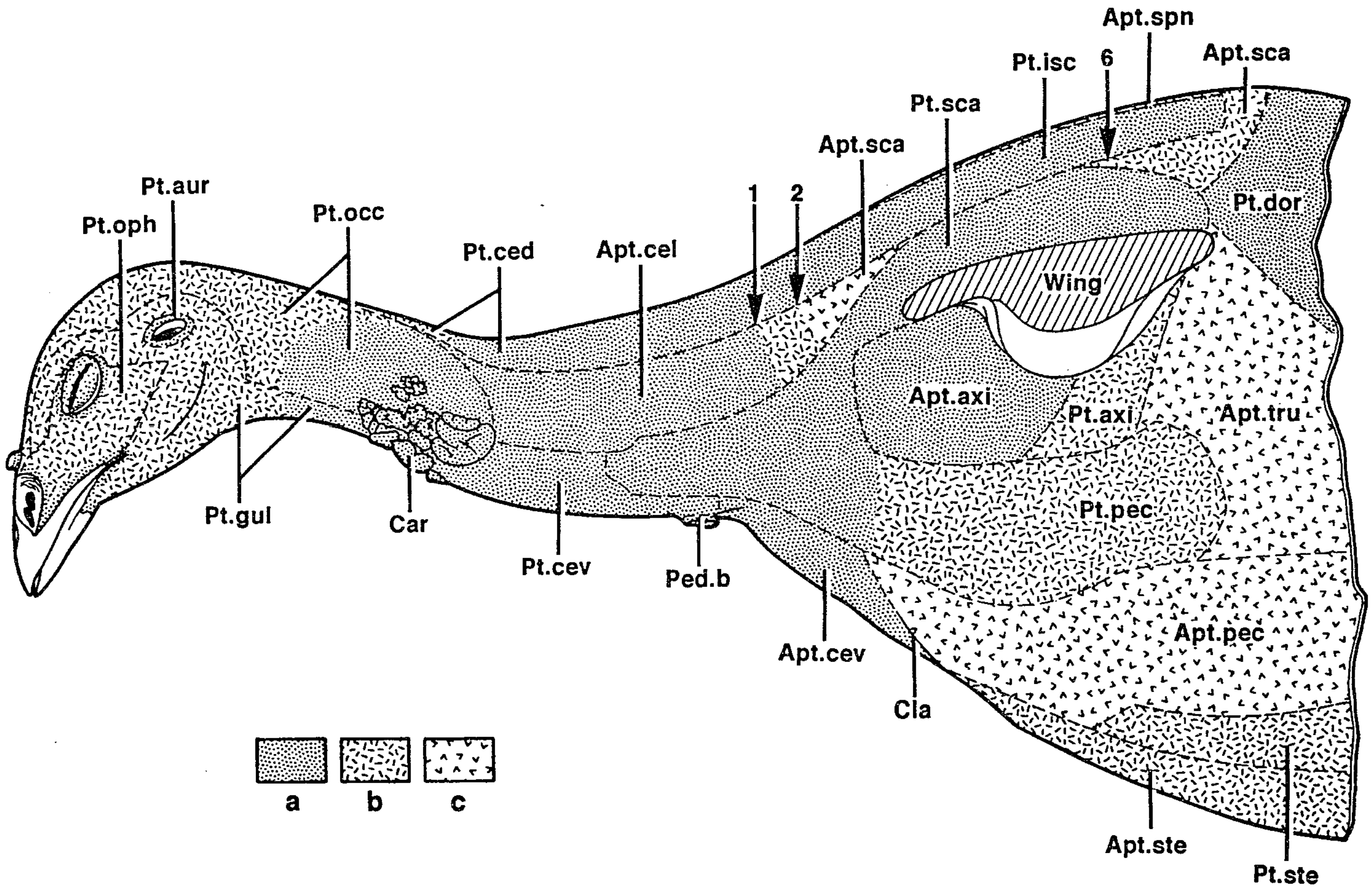
Figure 7. Diagram of a lateral view of the distribution of apterial muscles of the neck and thorax in Meleagris gallopavo. The thickness and density of the lines indicate the relative thickness and density of fiber bundles, and the length of dashes and spaces between indicate the relative lengths of the muscle and tendon segments of the fiber bundles. The borders between major overlying pterylae and apteria are indicated by dashed lines. Numerals: Levels of borderlines that coincide with borderlines identified by the same numbers in other figures. 3-4 extent of the part of M.apt.sca with very thick and dense fiber bundles; 4-5 extent of the part of the M.apt.sca with fiber bundles of intermediate thickness and density. Abbreviations: Apex palpable Apex carinae; Car overlying cervical caruncles; Cla palpable clavicle; cut cut edge of skin; M.apt.axi M. apterialis axillaris; M.apt.cel M. apterialis cervicalis lateralis; M.apt.cev M. apterialis cervicalis ventralis; M.apt.pec M. apterialis pectoralis; M.apt.sca M. apterialis scapularis; M.apt.spn M. apterialis spinalis M.apt.ste M. apterialis sternalis; M.apt.tru M. apterialis truncalis; Ped.b peduncles of beard; Pt.axi Pteryla axillaris; Pt.ced Pteryla cervicalis dorsalis; Pt.cev Pteryla cervicalis ventralis; Pt.dor Pteryla dorsalis; Pt.isc Pteryla interscapularis; Pt.occ Pteryla occipitalis; Pt.pec Pteryla pectoralis; Pt. sca Pteryla scapularis; Pt.ste Pteryla sternalis; Wing cross-section through base of wing.



M.apt.spn
M.apt.sca
Pt.isc
Pt.dor
Pt.sca
M.apt.sca
4
5
1
2
M.apt.cel
Pt.occ
Pt.ced
Wing
M.apt.tru
M.apt.axi
Pt.axi
Pt.pec
Car
Cut
Pt.cev
Ped.b
M.apt.cev
M.apt.tru
Cla
Apex
M.apt.ste
Pt.ste


Figure 7

Figure 8. Diagram of a lateral view of the distribution pattern of different interconnections between the cutis and the Fascia superficialis of the head, neck and thorax in Meleagris gallopavo. The borders between major overlying pterylae and apteria are indicated by dashed lines. Symbols: a fusion; b tight connection; c loose connection. Numerals: Levels of borderlines that coincide with borderlines identified by the same numbers in other figures. Abbreviations: Apt.axi Apterium axillare; Apt.cel Apterium cervicale laterale; Apt.cev Apterium cervicale ventrale; Apt.pec Apterium pectorale; Apt.sca Apterium scapulare; Apt.spn Apterium spinale; Apt.ste Apterium sternale; Apt.tru Apterium truncale; Car overlying cervical caruncles; Cla palpable clavicle; Ped.b peduncle of beard; Pt.aur Pteryla auricularis; Pt.axi Pteryla axillaris; Pt.ced Pteryla cervicalis dorsalis; Pt.cev Pteryla cervicalis ventralis; Pt.dor Pteryla dorsalis; Pt.gul Pteryla gularis; Pt.isc Pteryla interscapularis; Pt.occ Pteryla occipitalis; Pt.oph Pteryla ophthalmica; Pt.pec Pteryla pectoralis; Pt. sca Pteryla scapularis; Pt.ste Pteryla sternalis; Wing cross-section through base of wing.


Apt.spn
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Pt.isc
6
Pt.sca
Apt.sca
Pt.aur
Pt.oph
Pt.occ
Pt.ced
Apt.cel
1
2
Pt.dor
Wing
Apt.axi
Pt.axi
Apt.tru
Pt.gul
Car
Pt.cev
Ped.b
Pt.pec
Apt.cev
Cla
Apt.pec
a
b
c
Apt.ste
Pt.ste

Figure 8

Figure 9. Diagram of a lateral view of the variation pattern of the Fascia superficialis of the head, neck and thorax in Meleagris gallopavo. The borders between major overlying pterylae and apteria are indicated by dashed lines. A: Distribution pattern of different thicknesses. B: Location of fat bodies. Symbols: a thin fascia; b intermediate fascia; c thick fascia; c' thick fascia underlaid by the Lamina longitudinalis of the Fascia superficialis; d fat body enclosed in fascia fused with the Fascia constrictor; e fat bodies enclosed in Fascia superficialis alone. Numerals: Levels of borderlines that coincide with borderlines identified by the same numbers in other figures. Abbreviations: Arc.j palpable jugular arch; Apt.axi Apterium axillare; Apt.cel Apterium cervicale laterale; Apt.cev Apterium cervicale ventrale; Apt.pec Apterium pectorale; Apt.sca Apterium scapulare; Apt.ste Apterium sternale; Apt.tru Apterium truncale; C.csca Corpus adiposum cervicoscapulare; C.fac Corpus adiposum faciale; C.ral Corpus adiposum retroalare; C.sbal Corpus adiposum subalare; C.spal Corpus adiposum supraalare; Car overlying cervical caruncles; Cla palpable clavicle; M.lat.d. M. latissimus dorsi cranialis; M.sb.abdal M. subcutaneus abdominoalaris; M.sb.dor M. subcutaneus dorsalis; M.doral M. subcutaneus dorsoalaris; M.thoral M. subcutaneus thoracoalaris; Hy palpable hyoid horn; Ear external ear opening; Ped.b peduncle of beard; Pt.axi Pteryla axillaris; Pt.ced Pteryla cervicalis dorsalis; Pt.cev Pteryla cervicalis ventralis; Pt.dor Pteryla dorsalis; Pt.gul Pteryla gularis; Pt.isc Pteryla interscapularis; Pt.occ Pteryla occipitalis; Pt.oph Pteryla ophthalmica; Pt.pec Pteryla pectoralis; Pt. sca Pteryla scapularis; Pt.ste Pteryla sternalis; Wing cross-section through base of wing.

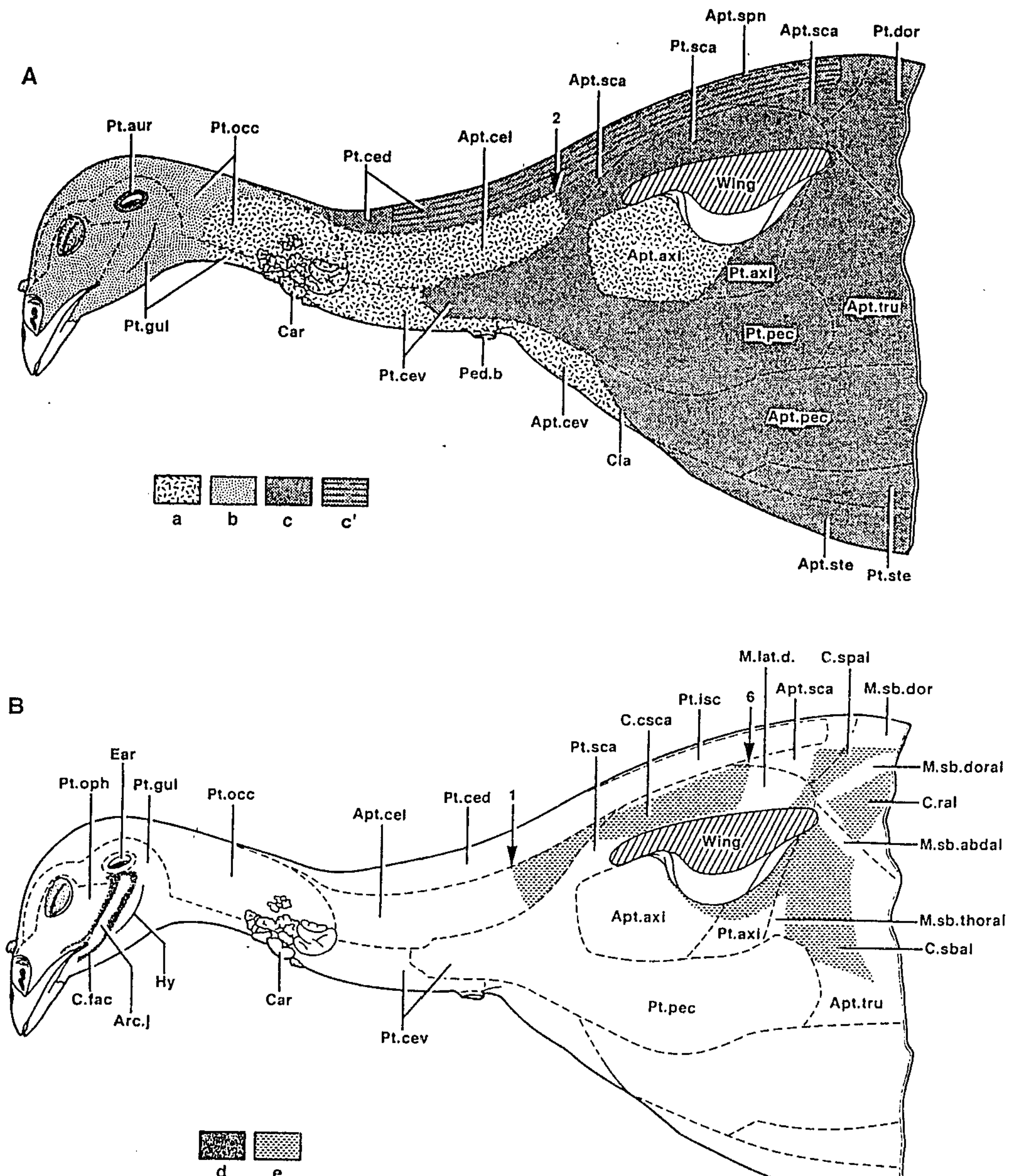
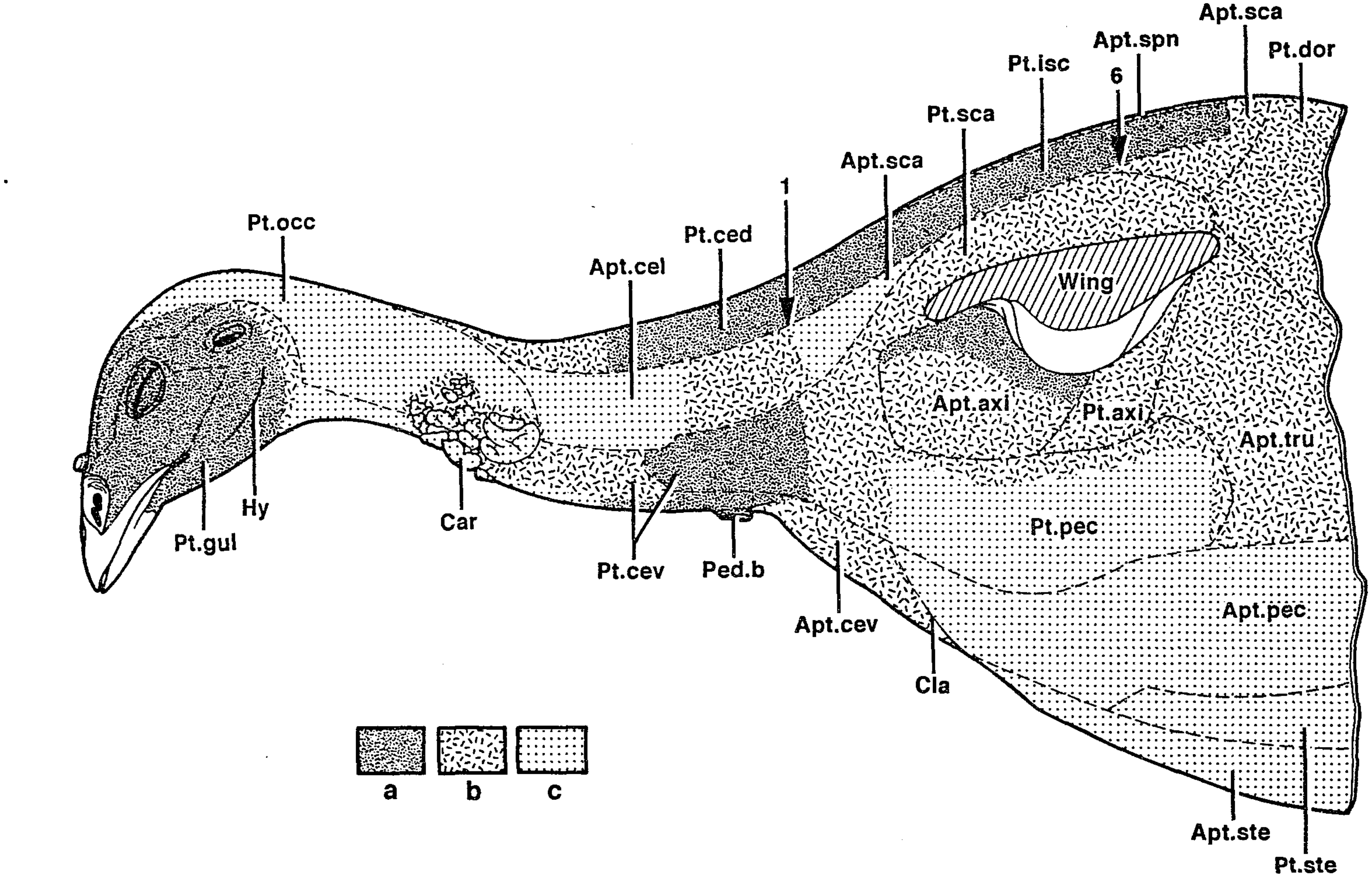

A
Apt.spn
Apt.sca
Pt.dor
Pt.sca
Apt.sca
Pt.aur
Pt.occ
2
Apt.cel
Pt.ced
Wing
Apt.axl
Pt.axl
Apt.tru
Pt.pec
Pt.gul
Car
Pt.cev
Ped.b
Apt.cev
Apt.pec
Cla
a
b
c
c'
Apt.ste
Pt.ste
B
M.lat.d.
C.spal
Apt.sca
M.sb.dor
Pt.isc
6
C.csca
Pt.sca
M.sb.doral
C.ral
Ear
Pt.oph
Pt.gul
Pt.occ
Apt.cel
Pt.ced
1
Wing
M.sb.abdal
Apt.axl
Pt.axl
M.sb.thoral
C.sbal
Hy
C.fac
Arc.j
Car
Pt.pec
Apt.tru
Pt.cev
d
e

Figure 9

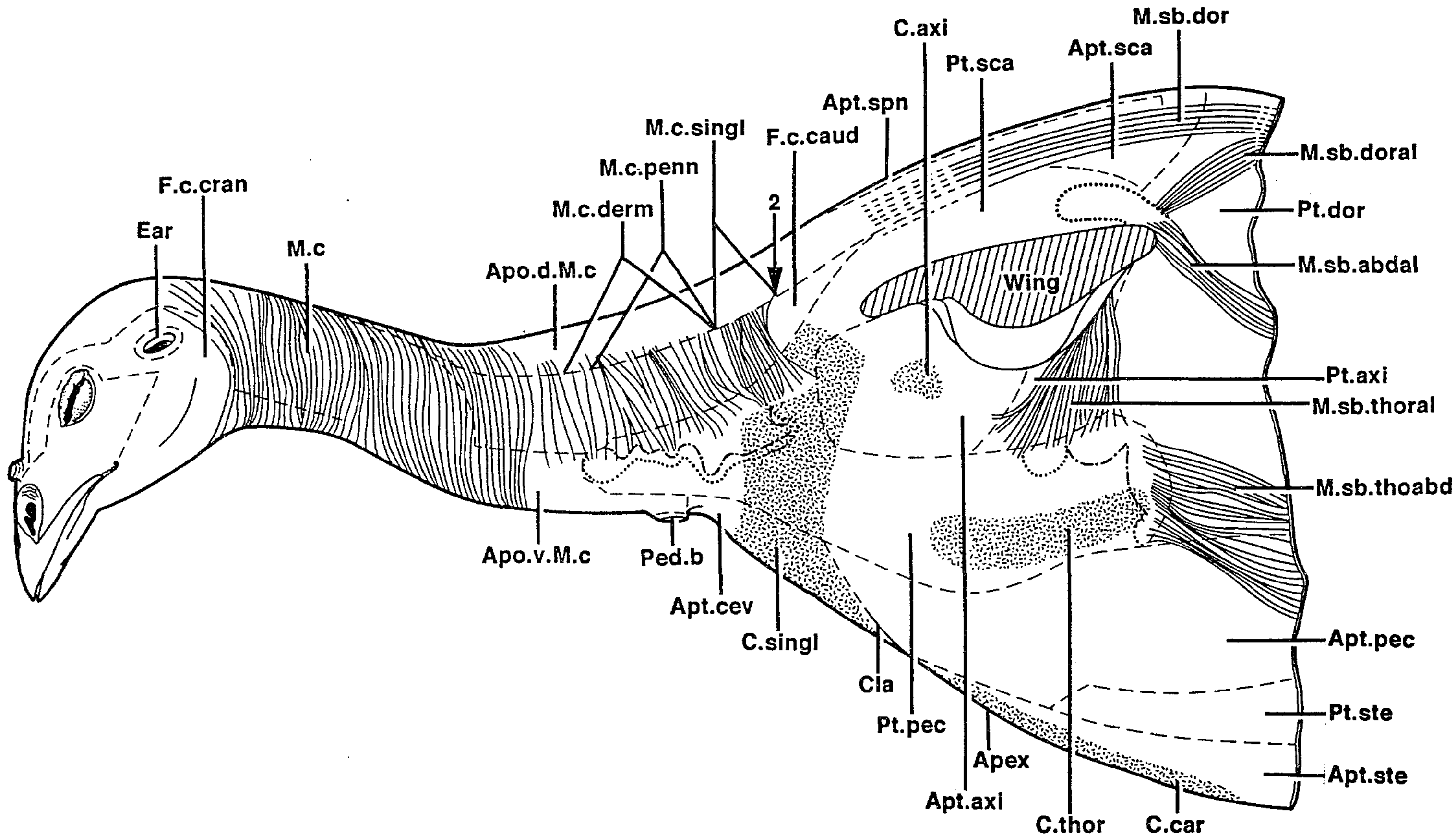
Figure 10. Diagram of a lateral view of the distribution pattern of different interconnections between the Fascia superficialis and the constrictor layer of the head, neck and thorax in Meleagris gallopavo. The borders between major overlying pterylae and apteria are indicated by dashed lines. Symbols: a fusion; b tight connection; c loose connection. Numerals: Levels of borderlines that coincide with borderlines identified by the same numbers in other figures. Abbreviations: Apt.axi Apterium axillare; Apt.cel Apterium cervicale laterale; Apt.cev Apterium cervicale ventrale; Apt.pec Apterium pectorale; Apt.sca Apterium scapulare; Apt.spn Apterium spinale; Apt.ste Apterium sternale; Apt.tru Apterium truncale; Car overlying cervical caruncles; Cla palpable clavicle; Hy palpable hyoid horn; Ped.b peduncle of beard; Pt.axi Pteryla axillaris; Pt.ced Pteryla cervicalis dorsalis; Pt.cev Pteryla cervicalis ventralis; Pt.dor Pteryla dorsalis; Pt.gul Pteryla gularis; Pt.isc Pteryla interscapularis; Pt.occ Pteryla occipitalis; Pt.pec Pteryla pectoralis; Pt. sca Pteryla scapularis; Pt.ste Pteryla sternalis; Wing cross-section through base of wing.



Apt.sca
Apt.spn
Pt.dor
Pt.isc
6
Pt.sca
Apt.sca
1
Pt.occ
Pt.ced
Apt.cel
Wing
Apt.axi
Pt.axi
Apt.tru
Hy
Pt.gul
Car
Pt.cev
Ped.b
Pt.pec
Apt.cev
Apt.pec
Cla
a
b
c
Apt.ste
Pt.ste


Figure 10

Figure 11. Diagram of a lateral view of the distribution of the striated subcutaneous muscles and fat bodies of the constrictor layer of the head, neck, and thorax in Meleagris gallopavo. The borders between major overlying pterylae and apteria are indicated by dashed lines. The borderlines of the insertions of the partes pennarum of subcutaneous muscles on feather follicles are indicated by dashed-dotted lines, and the borderlines of the insertions of the partes dermis on the cutis are indicated by dotted lines. Numerals: Levels of borderlines that coincide with borderlines identified by the same numbers in other figures. Abbreviations: Apex palpable Apex carina; Apo.d.M.c dorsal aponeurosis of M. constrictor; Apo.v.M.c ventral aponeurosis of M. constrictor; F.c.caud Fascia constrictor caudalis; F.c.cran Fascia constrictor cranialis; C.axi Corpus adiposum axillare; C.car Corpus adiposum carinae; C.singl Corpus adiposum supraingluviale; C.thor Corpus adiposum thoracale; Cla palpable clavicle; Ear ear; Apt.axi Apterium axillaris; Apt.cev Apterium cervicale ventrale; Apt.pec Apterium pectorale; Apt.sca Apterium scapulare; Apt.spn Apterium spinale; Apt.ste Apterium sternale; Apt.tru Apterium truncale; Hy palpable hyoid horn; M.c M. constrictor; M.c.derm pars dermis of M. constrictor; M.c.penn pars pennarum of M. constrictor; M.c.singl pars supraingluvialis of M. constrictor; M.sb.abdal M. subcutaneous abdominoalaris; M.sb.dor M. subcutaneous dorsalis; M.sb.doral M. subcutaneous dorsoalaris; M.sb.thoabd M. subcutaneous thoracoabdominalis; M.sb.thoral M. subcutaneous thoracoalaris; Ped.b peduncle of the beard; Pt.axi Pteryla axillaris; Pt.dor Pteryla dorsalis; Pt.pec Pteryla pectoralis; Pt.sca Pteryla scapularis; Pt.ste Pteryla sternalis.


M.sb.dor
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Apt.sca
Pt.sca
Apt.spn
M.c.singl
F.c.caud
M.sb.doral
M.c.penn
F.c.cran
2
Pt.dor
M.c.derm
Ear
M.c
M.sb.abdal
Apo.d.M.c
Wing
Pt.axi
M.sb.thoral
M.sb.thoabd
Apo.v.M.c
Ped.b
Apt.cev
C.singl
Apt.pec
Cla
Pt.ste
Pt.pec
Apex
Apt.ste
Apt.axi
C.thor
C.car

Figure 11

Figure 12. Montage of photomicrographs showing some fascicles of the pars pennarum of the M. constrictor inserting on some of the larger feather follicles of the ventral cervical feather tract of Meleagris gallopavo (DGH1♀). The bottom left corner shows the internal surface of the reflected Fascia superficialis and a transversely cut feather follicle. Scale bar= 10 mm.

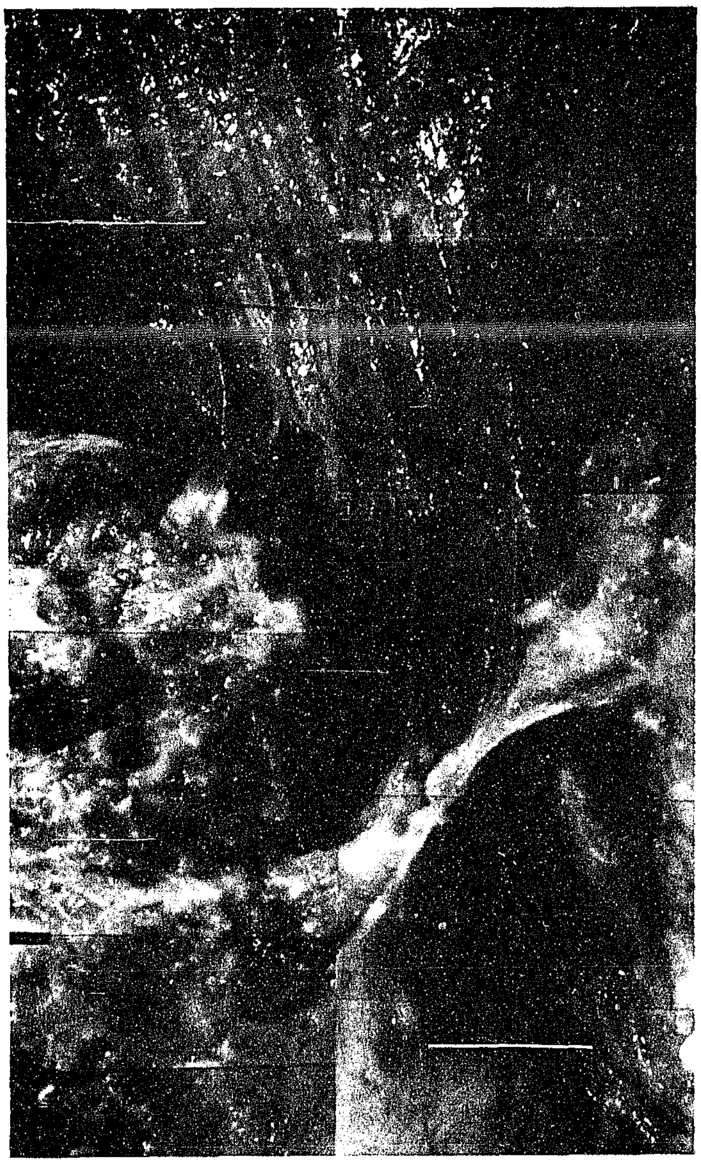
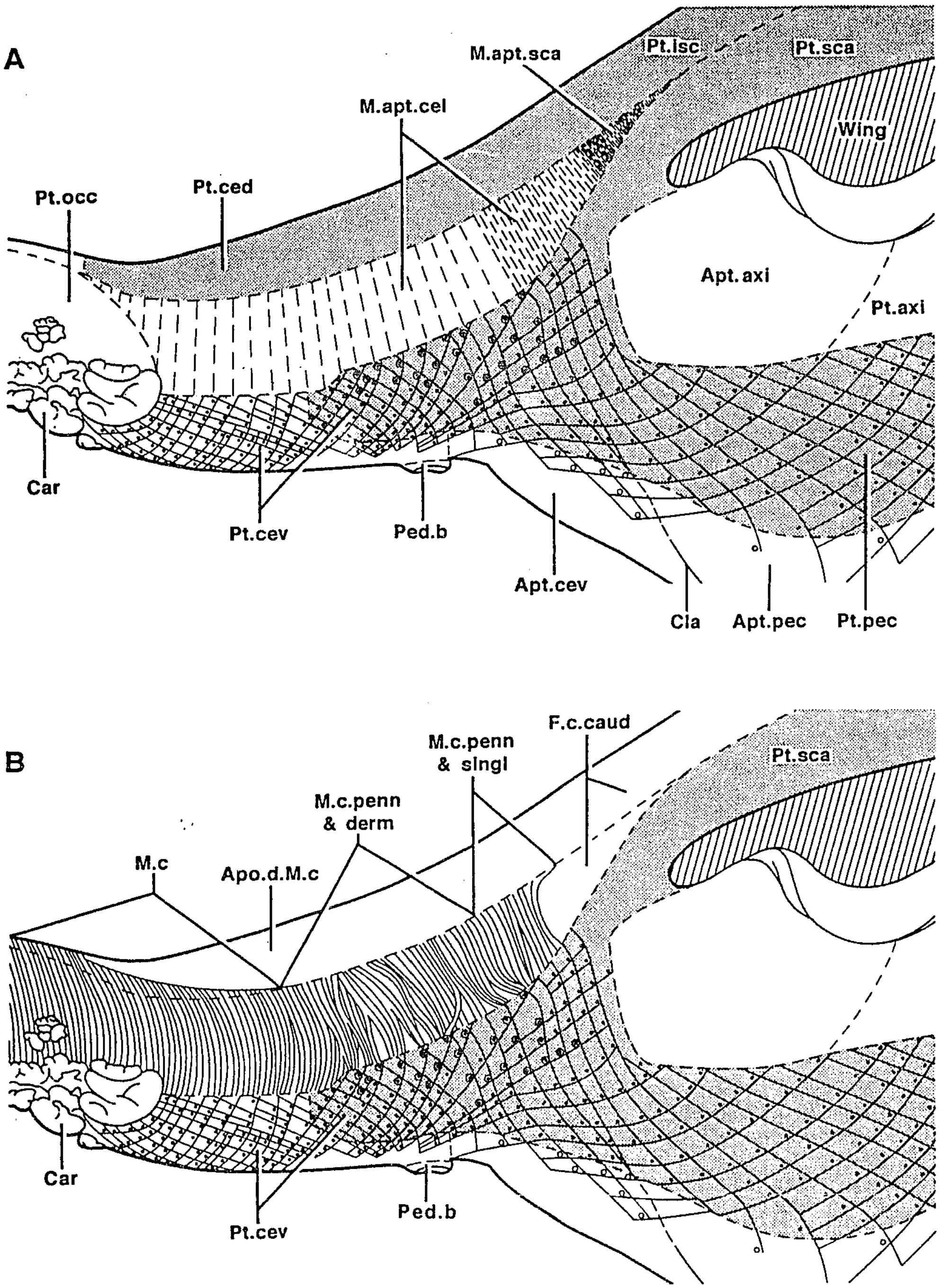


Figure 12

Figure 13. Diagrams of the lateral views of the caudal half of the neck and the cranial half of the thorax in Meleagris gallopavo, to illustrate the structural and functional relationships between the apterial muscles and the M. constrictor. The grid of diagonally crossing lines highlights the orientation of the feather rows and allows the identification of individual feather follicles. This grid and the individual feathers are shown only for the ventral cervical and pectoral feather tracts. The borders between pterylae and apteria are indicated by dashed lines. A: Lateral cervical and scapular apterial muscles connecting the dorsal and ventral cervical feather tracts. The different densities of lines indicate the different densities of fiber bundles. B: The M. constrictor, its dorsal aponeurosis, and its caudal fascia revealed after removal of the dorsal cervical feather tract and the lateral cervical and scapular apterial muscles. Symbols: Shaded areas highlight feather tracts with large contour feathers and underlaid by a subepidermal fat pad; solid dots represent follicles of contour feathers; solid dots in circles represent feather follicles to which the M. constrictor pars pennarum attaches; small circles represent follicles of semiplumes. Abbreviations: Apo.d.M.c dorsal aponeurosis of M. constrictor; Apt.axi Apterium axillare; Apt.cev Apterium cervicale ventrale; Apt.pec Apterium pectorale; Car overlying cervical caruncles; Cla palpable clavicle; F.c.caud caudal Fascia constrictor; M.apt.cel. M. apterialis cervicalis lateralis; M.apt.sca M. apterialis scapularis; M.c M. constrictor; M.c.penn & derm M. constrictor pars pennarum & pars dermis; M.c.penn & singl M. constrictor pars pennarum & pars supraingluvialis; Ped.b peduncle of beard; Pt.axi Pteryla axillaris; Pt.ced Pteryla cervicalis dorsalis; Pt.cev Pteryla cervicalis ventralis; Pt.isc Pteryla interscapularis; Pt.occ Pteryla occipitalis; Pt.pec Pteryla pectoralis; Pt. sca Pteryla scapularis; Wing cross-section through base of wing.


A
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Pt.isc
Pt.sca
M.apt.cel
Wing
Pt.occ
Pt.ced
Apt.axi
Pt.axi
Car
Pt.cev
Ped.b
Apt.cev
Cla
Apt.pec
Pt.pec
B
F.c.caud
M.c.penn
& singl
Pt.sca
M.c.penn
& derm
M.c
Apo.d.M.c
Car
Pt.cev
Ped.b

Figure 13

Figure 14. Diagram of the mechanism of feather movement.

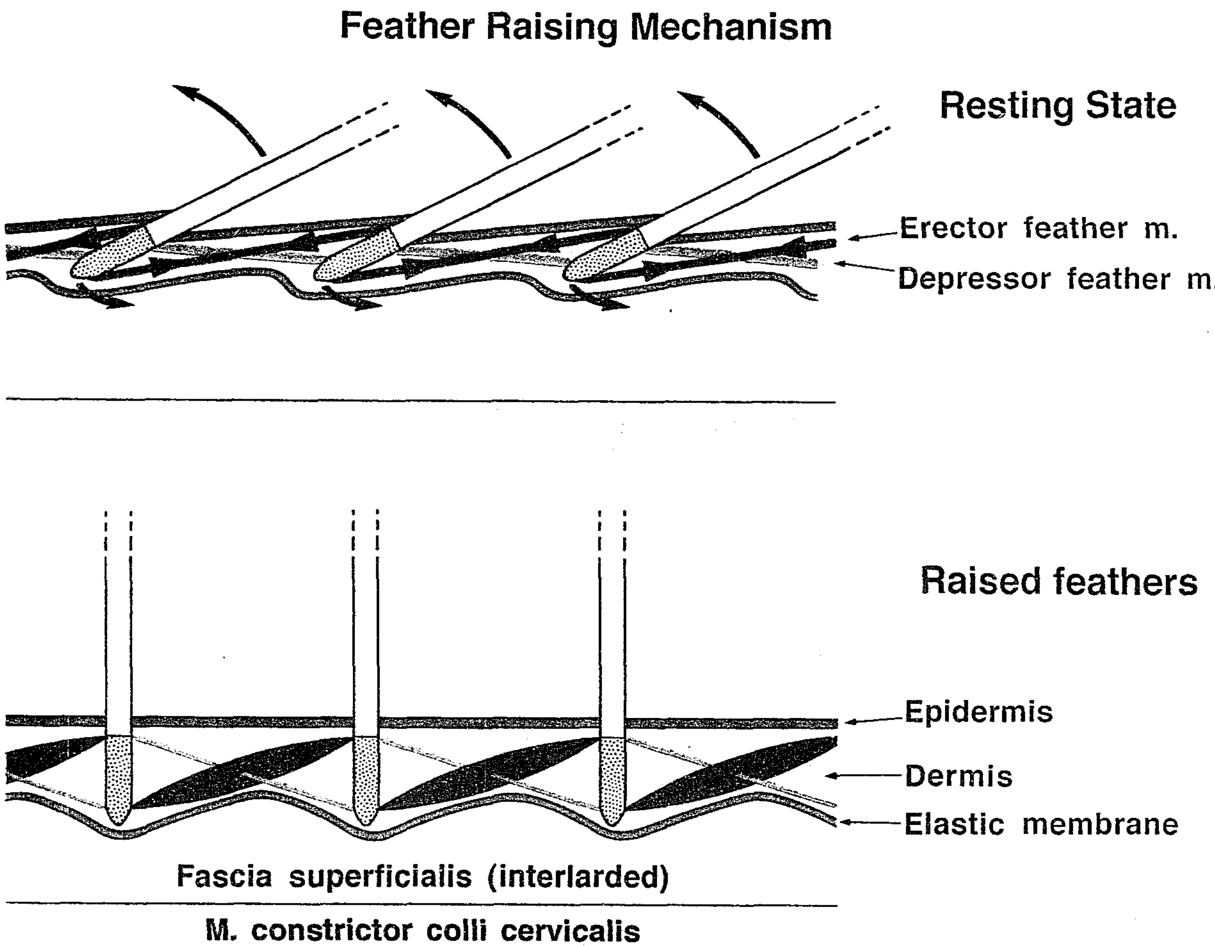
Feather Raising Mechanism
Resting State
Erector feather m.
Depressor feather m.
Raised feathers
Epidermis
Dermis
Elastic membrane
Fascia superficialis (interlarded)
M. constrictor colli cervicalis

Figure 14

## VITA

Kumudini Nishantha de Silva was born in Colombo, Sri Lanka on July 28, 1962 to Eric Jackson de Silva and the late Trixie Irene de Silva. She completed her high school at Vishaka Vidyalaya in 1981. In 1982, she was awarded the Indian Cultural Scholarship to study medicine in India and was also offered admission at the North Colombo Medical College in Sri Lanka. But she chose to pursue instead a career in basic science at the University of Colombo in Sri Lanka. In 1987, she graduated with a B.Sc. Honors degree in Zoology and joined the Faculty of Applied Science at the University of Sri Jayewardenepura in Sri Lanka as an assistant lecturer. In 1988, she was awarded a President's Scholarship from the Government of Sri Lanka and a Fulbright Scholarship to pursue a M.S. degree in Entomology at Louisiana State University. She received her M.S. degree in 1991. She then entered the Department of Zoology where she is presently a Ph.D. candidate in zoology.

## DOCTORAL EXAMINATION AND DISSERTATION REPORT

**Candidate:** Kumudini Nishantha de Silva

**Major Field:** Zoology

**Title of Dissertation:** Functional Anatomy of the Integument and Subcutaneous Structures of the Head, Neck and Thorax of the Domestic Turkey, <u>Meleagris gallopavo</u>

**Approved:**

D. J. Hillmann

**Major Professor and Chairman**

**Dean of the Graduate School**

**EXAMINING COMMITTEE:**

D. J. Hillmann

Harold Sherman

Yongmun Cho

Judith A. Schmidt

**Date of Examination:**

July 12, 1995